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Survival, behavior, use of territories, and breeding densities of male blue grouse in coastal British Columbia

by

Richard Arnold Lewis

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Survival, behavior, use of territories, and breeding densities of male blue grouse in coastal British Columbia submitted by Richard Arnold Lewis in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

Fred C. Zwickel
Supervisor

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....

Lewis W. Oring
External Examiner

Date March 13, 1984

Abstract

Survival and behavior of male blue grouse (*Dendragapus obscurus fuliginosus*) and ~~their~~ use of territories were examined in two populations in coastal British Columbia. Results were interpreted in relation to the role of these variables in determining densities of breeding males.

Data from a long-term study on Vancouver Island indicated that two-year-old and older males had an average annual mortality rate of 28%, and at two years of age life-expectancy was 3.1 years. At least 22% of two-year-old males were non-territorial (i.e., delayed breeding) and these birds survived as well as males that took territories. Of non-territorial males that survived, 40-45% subsequently obtained high quality territorial sites. Non-territorial adult males were present in a population on Hardwicke Island and they also survived as well as territorial birds. These results are consistent with the hypothesis that it is advantageous to delay breeding if high quality territorial sites cannot be obtained.

Ten territorial males were radio-tagged on Hardwicke Island and their movements monitored throughout spring and summer, 1981. Males concentrated their movements within or near the activity centers of their territories during the main period of breeding. Following peak breeding larger areas were used. Territory size was not related to relative aggressiveness of residents, as determined by playback experiments, but was inversely related to the amount of time

they spent hooting (singing).

Relative aggressiveness of residents was not related to the quality of territorial site occupied, suggesting that aggressiveness may not be a factor determining the quality of territorial site that is obtained; experience and behavior as a yearling may be more important. In one of two years, males occupying high quality sites hooted more and had more females sighted near them than those on poorer areas. Incidence of hooting, therefore, may affect a male's success in attracting females.

Habitat characteristics were compared between areas used and not used for territories, and between high and low quality sites. Males appeared to distinguish between sites that were and were not suitable for territories primarily on the basis of topography. However, when selecting among territorial sites for high quality areas, both topographic and vegetative characteristics seemed important. Preferences were related most to relative height of, amount and dispersion of cover, and visibility within, activity centers.

Habitat characteristics of territorial sites used by an interior race of blue grouse, *D. o. pallidus*, were relatively similar to those of *D. o. fuliginosus*. However, vegetative features may be more important in territorial site selection in interior races than in coastal races.

Overall, a combination of differences in behavior and movement patterns of yearlings and territorial behavior by adults, which results in some males delaying breeding, appears to be the mechanism through which densities of breeding males are regulated. However, the factor that ultimately sets limits to their numbers is not as well understood. Habitat does not appear to directly limit densities of breeding males. However, if numbers of breeding males are related to those of females, habitat may limit them indirectly through its effect on females. A removal experiment demonstrated that density and breeding success of females were not affected by numbers of males. The converse experiment, which would test for the effect of female numbers on males, has not been conducted.

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I express sincere thanks and gratitude to my supervisor, F. C. Zwickel, who throughout the course of my graduate program maintained a close interest in my research and always was available for discussion. Other members of my supervisory commitee, G. H. LaRoi and A. R. Palmer, as well as J. F. Bendell (University of Toronto), D. A. Boag (University of Alberta), S. J. Hannon (University of California, Berkeley), J. Hines (University of Alberta), I. G. Jamieson (University of Alberta), D. M. Keppie (University of New Brunswick), K. Martin (Queen's University), D. T. McKinnon (University of Alberta), J. O. Murie (University of Alberta), and L. W. Oring (University of North Dakota) also provided many helpful suggestions and discussions. Many people assisted in collecting field data, of whom I especially thank F. Backhouse, M. A. Degner, S. J. Hannon, R. D. Holmes, M. T. Nietfeld, C. E. Thompson, and D. M. Walsh. F. C. Zwickel provided a pointing dog which proved to be not only immeasureably beneficial but also an amiable field companion.

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permission of the Washington State Department of Game. Financial support was provided by the Natural Sciences and Engineering Research Council of Canada, the University of Alberta, and the British Columbia Fish and Wildlife Branch.

Finally, but by no means least, I extend sincerest and warmest thanks to my parents, Mr. and Mrs. W. A. Lewis, as they unendingly encouraged my education and always provided moral support when it was needed.

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Introduction

Territorial behavior may regulate densities of breeders in many species (e.g., Orians 1961, Tompa 1962, Carrick 1963, Krebs 1971, Zimmerman 1971), but until recently this was not considered true for male blue grouse (*Dendragapus obscurus fuliginosus*) (Bendell and Elliott 1967, Zwickel 1972). This conclusion was based on the belief that all adult males took territories. Current research has shown this to be erroneous (Lewis and Zwickel 1980, Jamieson and Zwickel 1983), however, as some males apparently forego attempts at breeding if they cannot obtain high quality territorial sites. However, we do not know what determines which males acquire the best territorial sites, or the fate of birds that delay breeding. As well, we know little about habitat differences that give rise to differences in quality among territorial sites (Lewis 1981). My objective was to study aspects of territoriality in males that might help answer these questions. Ultimately the goal was to improve our understanding of how densities of breeding males are determined. I present my results in 5 papers and 2 appendices:

1. Survival and delayed breeding in male blue grouse.
2. Use of space by territorial male blue grouse.
3. Behavior of male blue grouse and its relation to quality of territory occupied and attraction of females.
4. Density, movements, and breeding success of females in an area of reduced male density.

5. Habitat preferences of territorial male blue grouse.

Appendix I: Further evidence of non-territorial adult male blue grouse.

Appendix II: Territorial sites of pallid blue grouse, *Dendragapus obscurus pallidus*.

In the first paper I examine and compare survival of territorial and non-territorial individuals, and document the fate of males that delay breeding. I examine the use of space by territorial males in paper 2, and in paper 3, I compare aggressiveness and incidence of hooting (singing) of males on high and low quality territorial sites. In the latter paper, I examine behavior of males in relation to quality of territorial sites occupied and attraction of females. As part of my study, I classified territorial sites as to quality by removing territorial and subsequent replacement males (Lewis and Zwickel 1980). This enabled me to address the question of how densities of males affect densities and breeding success of females, and these results are presented in paper 4. In paper 5, I compare habitat characteristics of territorial sites to areas not used for territories, and within areas used for territories, between those that were preferred and non-preferred. Differences are interpreted in relation to how they might affect survival and breeding success of residents.

Information on presence and survival of non-territorial adults was from long-term studies on Vancouver Island whereas most of my current field studies were carried out on

Hardwicke Island, British Columbia during 1980-1982. I document the occurrence and fate of non-territorial adults in the latter population in Appendix I. Appendix II describes territorial sites of pallid blue grouse (*D. o. pallidus*) in north-central Washington State. This subspecies occupies habitats that are vastly different from those occupied by *D. o. fuliginosus* in coastal British Columbia. Though not directly related to the question of population regulation, this information is relevant to the overall problem of territorial site selection in blue grouse.

General theories on how densities of breeding animals are determined are presented in a concluding discussion. I then integrate my results with those of other studies on blue grouse and consider them in relation to these theories.

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Paper 1: Survival and delayed breeding in male blue grouse[1]

Abstract

We present an analysis of survival of male blue grouse (*Dendragapus obscurus*) using known-aged individuals and examine the results in terms of the evolution of delayed breeding. Males had low rates of mortality and, among two-year-olds, mortality rates of territorial and non-territorial birds were the same. Up to six years of age, males had life expectancies of at least two years. Males that postponed breeding and survived had a 40-45% chance of eventually obtaining a high quality site for a territory. If males had not delayed breeding they likely would have had to settle on areas where opportunities for breeding appear to be low. Thus, survival patterns of males are consistent with the hypothesis that it is advantageous for some males to delay breeding if high quality sites cannot be obtained.

---

[1] co-authored with F. C. Zwickel.

Introduction

Blue grouse have a mating system in which males are territorial and promiscuous (Bendell and Elliott 1967, Wiley 1974a). Most yearling and some adult males are non-territorial (Wiley 1974a, Wittenberger 1978, Lewis and Zwickel 1980). In studies on Vancouver Island these males were considered to be delaying breeding as they were physiologically able to reproduce (Hannon *et al.* 1979) yet did not take territories even though vacant territorial sites always were present (Lewis and Zwickel 1981); occupancy of a territory is considered prerequisite for breeding. However, the space that was available was of low quality. Males that occupied low quality areas survived less well and had fewer opportunities to encounter females than those on high quality sites. Thus, we postulated that yearlings and some adults that are unable to obtain high quality sites gain more, in the long term, if they delayed breeding than if they took territories on poorer areas. A removal experiment demonstrated that non-territorial adults and at least some yearlings will occupy prime sites if they are available (Lewis and Zwickel 1980).

For a system of delayed breeding to evolve, individuals that do so ultimately must produce as many offspring as those that attempt to breed at an earlier age (Selander 1965). Wiley (1974b) demonstrated that this can occur if early survival and (or) later fecundity are enhanced by not attempting to breed at the earliest possible time. To evaluate properly whether or not delayed breeding is selectively advantageous, however, the overall reproductive success of an individual would have to be compared to its success if it had not postponed breeding. Since this is impossible, indirect evidence must be used to explain the evolution of delayed breeding.

Although we have suggested that it is advantageous for yearlings and some adults to delay breeding if they are unable to obtain high quality sites for territories, this explanation is not complete until other questions also are answered. First, one must demonstrate that some, if not most, males that delay breeding survive and second, that some of these birds obtain high quality sites. As well, in our earlier examination of male survival, we only considered average survival (Lewis and Zwickel 1981). The relative magnitude of mortality in different age classes also is relevant to explanations for delayed breeding. For example, delayed breeding would be more likely to evolve in species that have low mortality throughout their life than in species that suffer high early mortality but survive well in later years.

Here we examine these questions through an analysis of territorial occupancy and survival of known-aged males, and discuss the results in relation to the evolution of delayed breeding.

Study area and methods

Comox Burn, on the east slope of Vancouver Island, was used as the study area. It has been described in detail by Zwickel and Bendell (1967, 1972) and Zwickel (1977). Blue grouse were studied intensively from late March or early April to late August each year from 1969 to 1978 and from early April to 31 May in 1979. Some grouse also were banded in 1968 and a partial census was conducted in 1980.

Two methods were used to mark individuals: 1) small numbered metal tags were attached to the patagium of juveniles too small to hold leg bands, and 2) unique combinations of metal and colored plastic leg bands were placed on larger juveniles and older birds. Thus, exact ages of birds marked as juveniles or yearlings (Braun 1971) were known. The fates of marked individuals were determined using field techniques outlined by Zwickel and Bendell (1967) and Lewis and Zwickel (1981).

Although adult males tend to establish territories in areas they occupied as yearlings (Sopuck 1979), some yearling males seen on Comox Burn subsequently could have taken territories off the study area. Most areas immediately surrounding Comox Burn were censused but not as intensively as the main study area. Thus, accurate estimates for survival of yearling males cannot be calculated using data provided by this study. Once males take territories, however, they usually return to the same one, year after year until death (Lewis and Zwickel 1981). Hence, age at dying for territorial males was determined by observing when they disappeared.

We constructed a composite life table (Hickey 1952) for known-aged males that were two-years-old and older. Only males that were yearlings prior to 1976 were included in this analysis as some that were identified after 1975 were still alive in 1980 and their lifespans could not be determined. Average adult survival, as reported here, is slightly underestimated, however, because three long-lived males that were alive in 1980 and 10 males that were shot in a removal experiment in 1978 and 1979 (Lewis and Zwickel 1980) were included in the analysis.

Results

From 1968 to 1975, 141 yearling males were identified on Comox Burn. Seventy-eight (55%) were later seen as adults, 70 on Comox Burn. Three that were marked as juveniles, but not seen as yearlings, settled on the study area as adults, giving a total of 73 known-aged adults.

Sixteen of the adults (22%) did not take territories as two-year-olds. One was killed when recaptured and 12 of those remaining (80%) survived at least one more year. Of these, 11 took territories and the other was shot in the removal experiment as a "surplus" four-year-old. Five of the non-territorial two-year-olds (45%) subsequently acquired high quality sites for territories and six (55%) settled on low quality sites.

Age-specific mortality rates of adults were all less than 30% up to four years of age, and up to six years of age, males had life expectancies of two years or more (Table 1). The weighted average mortality rate for adults was 28% and at two years of age males had a life expectancy of 3.1 years (see Botkin and Miller (1974) for equations to estimate average mortality rates and average life expectancies). The oldest male represented in the life table died at 10 years of age, but this is not the longest males have been known to survive. One individual, banded as an adult, lived to at least 13 years of age.

The average age of males that died naturally was 4.3 years whereas the average age of those shot by us or still alive in 1980 was 6.4 years. Therefore, the overestimation of mortality rates that results from inclusion of these males in the analysis falls mostly in the older age classes. Because of this we cannot compare age-specific mortality rates of old and young adults. However, this does not affect the conclusion that young adults survive well and have relatively long life expectancies.

Elsewhere, we presented data showing that males occupying persistent sites lived significantly longer, on average, than those on transient sites (equivalent to high and low quality sites, respectively (Lewis and Zwickel 1981)). Though sample sizes were small, life tables for males on the two types of site showed that individuals acquiring persistent sites had longer life expectancies in all age classes than individuals taking territories on transient sites (Table 2). Weighted mean annual mortality rates for males on persistent and transient sites were 25% and 33%, and average life expectancies after two years of age were 3.5 and 2.5 years, respectively.

Discussion

A minimum of 55% of our yearling males survived and returned as adults. Zwickel and Bendell (1967) estimated that yearling males have a survival rate of 70%. Non-territorial, two-year-old males had a mortality rate of 20% (3/15), similar to that of two-year-olds that were territorial (16%, 9/58, $p > 0.50$). Thus, males, both yearling and adult, that did not take territories had a high probability of surviving. In contrast, non-territorial red grouse (*Lagopus lagopus scoticus*) are reported to have very high mortality rates (Watson 1964).

Since yearling males rarely take territories, we cannot determine what their mortality rate would be if they did. If being territorial reduces a yearling's chance of surviving, that also would be a factor selecting for delayed breeding in males in this age class.

Since almost all high quality sites are occupied each year (Lewis and Zwickel 1981), almost all males that postponed breeding would have had to select low quality sites had they taken territories. However, if it is advantageous for males to delay breeding if they do not acquire high quality sites, individuals that do so must have some chance of subsequently obtaining one of these areas. Forty percent of the yearlings that eventually acquired territories as adults (25/59, excluding those that changed territories from one year to the next) and 45% of the non-territorial two-year-olds later obtained high quality sites. Thus, almost half of the males that delayed breeding eventually were successful in obtaining high quality areas.

Two-year-old males had an average life expectancy of 3.1 years. Therefore, yearlings that survived still had, on average, three years in which to attempt to reproduce. Males up to the age of six years had life expectancies of two years or more. Thus, on average, young adults that delayed breeding would have the opportunity to try and breed in at least one future year.

Twenty-two percent of known two-year-old adults were non-territorial. Clearly only a portion of the males from this age class delay breeding while the rest take territories, some on transient sites. Decreasing life expectancies with age are likely involved with it being advantageous for adults to use poorer areas for territories if the best sites are not available. However, it remains to be explained why some two-year-olds do not take territories whereas others settle on transient sites. Perhaps males in this age class that do not obtain persistent sites initially, are equally successful by either settling on transient sites or by delaying breeding and obtaining a persistent site at a later date.

In summary, results from this study show that males that delayed breeding suffered low mortality, and that about half of those that survived eventually acquired high quality sites for territories. Further, males that postponed breeding and later took territories had, on average, one to three years in which to reproduce. These results provide additional support for our hypothesis that yearlings and some adults gain more by delaying breeding than by selecting transient sites for territories if high quality sites are unavailable. A more complete explanation for the evolution of delayed breeding in male blue grouse cannot be achieved until we can determine the relative frequencies with which males that occupy high and low quality sites breed.

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Table 1. Life table for males, two-years-old and older, that were yearlings on Comox Burn between 1968 and 1975.

Age	Number alive	Number dying	% dying	Life expectancy (years)
2	73	12	16	3.1
3	61	15	25	2.6
4	46	13	28	2.3
5	33	12	36	2.1
6	21	8	38	2.0
7	13	2	15	1.9
8	11	6	56	1.1
9	5	3	60	0.9
10	2	2	100	0.5

Table 2. Life tables for males that had territories on persistent and transient sites on Comox Burn and that were yearlings between 1968 and 1975. Males that changed the location of their territories from one year to the next are not included.

	Persistent sites				Transient sites			
Age	No. alive	No. dying	% dying	Life expect. (years)	No. alive	No. dying	% dying	Life expect. (years)
2	24	3	13	3.5	35	5	14	2.5
3	21	4	19	2.9	30	11	37	1.8
4	17	4	24	2.4	19	8	42	1.6
5	13	5	39	2.0	11	5	46	1.4
6	8	3	38	2.0	6	4	67	1.2
7	5	1	20	1.9	2	0	0	1.5
8	4	2	50	1.3	2	2	100	0.5
9	2	1	50	1.0				
10	1	1	100	0.5				

2

Paper 2: Use of space by territorial male blue grouse

Introduction

The social system and breeding behavior of blue grouse (*Dendragapus obscurus*) have been studied in several areas of coastal British Columbia with an emphasis on determining how these relate to the regulation of breeding densities (e.g., Bendell and Elliott 1967, Mossop 1971, Zwickel 1972, Bendell et al. 1972, Bergerud and Hemus 1975, Zwickel 1980). In short, adult males establish territories on breeding ranges in spring and from there advertise their presence to conspecifics by hooting (singing) (Bendell and Elliott 1967, McNicholl 1978). The mating system is considered promiscuous (Wiley 1974) with females not associating with males except, presumably, to breed.

Territories serve primarily as areas for display and mating, although feeding and other activities also occur there (Bendell and Elliott 1967, McNicholl 1978). Males spend much of their time hooting during the breeding season, usually from a few specific places within the territory; the area that encompasses these locations being the activity center (McNicholl 1978, Lewis and Zwickel 1981) of the territory. Following the breeding season, hooting declines (McNicholl 1978) and males migrate to winter ranges (Bendell and Elliott 1967).

In previous studies territorial males were found either by observers searching alone or with pointing dogs. With these methods hooting males are easier to find than silent males and there is a bias towards finding them within activity centers. I overcame this bias by radio-tagging territorial males and monitoring their movements throughout spring and summer. Thus, I was able to address questions fundamental to interpretations of the function of territories for male blue grouse. Specific questions that I asked were: 1) do territorial males remain within activity centers during peak breeding when not hooting?, 2) do territorial males use the same areas after peak breeding as they used during peak breeding?, and 3) what portion of a male's spring and summer home range should be considered his territory? Additionally, I determined the amount of time spent hooting by radio-tagged males, and assessed their relative aggressiveness by conducting playback experiments; differences among males in these behaviors may relate to differences in sizes of areas occupied (e.g., Watson and Miller 1971, Falls 1978).

Study area and methods

This study was conducted in 1981 on Hardwicke Island (77 sq km), which is situated between Vancouver Island and mainland British Columbia, approximately 80 km NW of Campbell River. This island is in the coastal western hemlock (*Tsuga heterophylla*) biogeoclimatic zone (Krajina 1965). My study area was approximately 56 ha in size and ranged in elevation from 330 to 500 m. The area had been logged recently and vegetation structure was "very open" to "open" (Bendell and Elliott 1967). Ground cover consisted primarily of burned or unburned slash, mixed grasses, fireweed (*Epilobium angustifolium*), and thickets of small trees, principally western hemlock and Douglas fir (*Pseudotsuga menziesii*).

From 8 to 16 April, 10 adult males were captured with snare poles (Zwickel and Bendell 1967) and equipped with radio transmitters using a harness attachment (Herzog 1979). One male was killed by a predator one week after being radio-tagged so on 24 April the transmitter was placed on another bird. Transmitters weighed 30± gms (less than 2.5% of a bird's weight), had a potential range of up to 3 km, and were applied only to males that had been hooting before capture or that had been seen as adults in former years (i.e., were considered to be territorial). Territorial males were found easily because of their hooting and most (10/15) on my study area were radio-tagged (Figure 1).

Radio-tagged birds were located with a receiver and hand-held yagi antenna, and their exact locations determined by taking a compass bearing and pacing to known reference points. Radio-tracking was conducted at least every three days, usually more often. Each day birds were tracked, an attempt was made to find all of them. Males were found relatively equally except for one with a faulty transmitter (no. 677) and two that were killed by predators (nos. 668 and 770, Table 1). Sightings by workers searching this area as part of a larger study increased the number of observations of radio-tagged males, but only to a small extent (6.8% of total observations). I monitored these birds until late August, by which time all had left their territories.

Below I refer to the area used by a male as an "area of occupancy" rather than as a territory. I do this because size of area used was examined for different time periods within the time males were territorial.

I examined and compared areas of occupancy from 8 April to 20 May, and from 21 May to 16 June. The first period included the time from radio-tagging of the first male until the end of peak breeding (F. C. Zwickel unpubl. data); the second was from the end of peak breeding to the date when the first male abandoned his territory. Although some breeding did occur after 20 May (7.3%), for simplicity I refer to these as the "breeding" and "post-breeding" periods, respectively. A third estimate of size of area occupied was for the time from radio-tagging until territories were abandoned. Comparisons among males for the total area used during this time are not completely standard since individual males abandoned territories on different dates.

Maximum areas used during these periods were delineated by connecting outermost points of observation with a straight line (Odum and Kuenzler 1955, Bendell and Elliott 1967). I also used a modified minimum area method (Harvey and Barbour 1965) to determine areas of occupancy but because results were similar I include only the former here. Activity centers were delineated by connecting outermost locations at which males were seen hooting.

Playback experiments were used to assess each male's "aggressiveness", or tendency to attack (Watson and Parr 1981). In each experiment, I placed a loudspeaker and mount of a male blue grouse in display posture 10 m from a territorial male and hid 10 m further away. After 10 minutes, I played a tape recording of another male's hooting for 10 minutes and noted all responses by the experimental male during that time. The same tape recording and mount were used for all experiments and none of the males had prior experience with either. All experiments were conducted after 20:00 from 11 to 20 May and in all but two, the males were hooting immediately before the experiment. I conducted only one experiment on each male as similar tests elsewhere on Hardwicke Island indicated that territorial males habituate rapidly to such playbacks (Lewis 1984a).

Pearson's product moment correlation coefficient or Spearman's rho was calculated to test for correlations between variables. Significance was accepted at the 0.05 probability level.

Results

All radio-tagged males except one were heard hooting and some were seen displaying to females or other males. Thus, radio-packages apparently did not disrupt singing or display behavior. Although one male was not heard hooting, I considered him to be territorial because his movements were localized compared to those of non-territorial males (Sopuck 1979, Jamieson 1983). Also, I may have missed hearing this male hoot because most radio-tracking was done between 9:00 and 17:00, when incidence of hooting is low (McNicholl 1978).

Size of areas occupied

During the breeding period, males occupied areas that ranged in size from 0.26 to 0.93 ha, and averaged 0.63 ha (Table 1). Sixty-four per cent (117/172) of the sightings were within activity centers, and activity centers comprised an average of 44% of the area used during this period.

Areas occupied during the post-breeding period averaged 1.07 ha in size, an increase of 71% over the peak breeding period (Table 1). The difference is significant if the two males killed by predators are excluded (paired t-test, t = 2.73, p = 0.03). Forty-one percent (70/173) of the sightings obtained during the post-breeding period were within activity centers, and 57% (99/173) were in areas used earlier. On average, 76% of areas occupied during the breeding period were used in the post-breeding period. Total areas used during both periods averaged 1.43 ha.

The larger areas used after peak breeding did not include a corresponding enlargement of activity centers; areas within which males were observed hooting increased only 7.1% when observations from the post-breeding period were added to earlier sightings.

Size of area occupied was not correlated with the number of sightings for each male in either period (breeding period: Spearmans's rho = 0.120, $p > 0.50$; post-breeding period: Spearman's rho = 0.177, $p > 0.50$). Males were found a similar number of times in both periods (Table 1) so the increase in size of area used after peak breeding did not result from a greater number of observations during that time.

Areas occupied during the entire time from radio-tagging until moving to new areas after the breeding season averaged 1.9 ha (Table 2). Only three instances of overlapping use of the same area by adjacent males occurred, with areas of overlap averaging 7.1% of the total area occupied by these males (Figure 1). There was no overlap among activity centers.

Abandonment of territories

Exact dates of departure from territories were known for four males and the others were estimated as the date midway between the last day seen on territory and the first day seen elsewhere (average time between these dates was

1.75 days). The first and last males to adandon territories did so on 17-18 June and 11 August, respectively, and others left at regular intervals between these dates (Table 2). Abandonment involved quick and direct moves to new areas, usually within two days or less. Three males moved to dense coniferous forest, typical of winter range, and the other five moved to new areas on the breeding range. The latter males again restricted their movements but did not behave territorially (i.e., were not observed to hoot or display). One later moved into dense conifers whereas the other four were still on summer range when radio-tracking was terminated in late August.

It was readily apparent when territories had been abandoned because long distance movements or movements to different habitats were involved. However, prior to abandoning territories seven sightings were obtained which I considered to be atypical (7/440, 1.6%). Four of these involved movements in which males had crossed the territories of other males, the other three were instances in which males were found in areas that were far from their usual areas of occupancy and that were uncharacteristic of areas in which territorial males usually were found during this time. In all cases, the males were back on their usual area of occupancy when next found. Such sightings may have resulted from males being chased by predators or from chasing conspecifics. I did not include these sightings in computations of areas of occupancy.

Aggressiveness and size of area occupied

Two males did not respond to the playback experiment and one approached and vigorously attacked the male mount. Responses by the others consisted of approaching to within varying distances of the speaker and mount, and in some cases uttering aggressive "growls" (Stirling and Bendell 1970). I assigned each male a score between zero and eight, with higher scores representing greater tendencies to approach and/or attack the male model; scores were based on closeness of approach, time spent near the mount, and response (vocalizations and attack) to the mount. No individuals received the same score except for the two that did not respond (Table 3), these being the two that were not hooting before the experiment. Since the tendency to attack may have been affected by whether or not an individual was hooting I made comparisons with and without the inclusion of these males.

The size of area males occupied during the peak breeding period was not related to their relative aggressiveness, as measured from playback experiments, except when the two males that were not hooting prior to the experiments were excluded (Spearman's rho = 0.786, $0.02 < p < 0.05$). As well, in neither case was relative aggressiveness significantly correlated with size of area used during the post-breeding period, the combined breeding and post-breeding periods, or the total time from radio-tagging until abandoning territories. Time of territorial abandonment and relative aggressiveness also were not correlated.

Time spent hooting and size of area occupied

Sightings by workers who were not radio-tracking were not included when determining percent of observations for which males were hooting because those workers were more likely to find hooting than non-hooting males. Although incidence of hooting varies throughout the day and seasonally (McNicholl 1978), that probably did not affect my results because: 1) males were found with relatively equal frequency up to 16 June, and 2) 92.8% of the sightings to this time were obtained between 09:00 and 18:00, when hourly hooting rates vary little (McNicholl 1978).

The percent of observations in which males were hooting (frequency of hooting) was not correlated with the size of area used during either the breeding or post-breeding periods ($r = -0.570$, $N = 10$, $0.05 < p < 0.10$, and $r = -0.339$, $N = 10$, $0.20 < p < 0.50$, respectively). However, total area used from 8 April to 16 June and from 8 April to territory abandonment were inversely related to a male's frequency of hooting ($r = -0.940$ and -0.803, respectively; both p's < 0.01).

Date of territory abandonment was not related to a male's frequency of hooting during either the breeding or combined breeding and post-breeding periods (Spearman's rho $= 0.241$, $N = 8$, $p > 0.50$, and Spearman's rho $= 0.371$, $N = 8$,

$0.20 < p < 0.50$, respectively). A male's relative aggressiveness also was not related to his frequency of hooting.

Discussion

Throughout the breeding and post-breeding periods the 10 radio-tagged males did not use all areas of their home range equally. During peak breeding, males spent much of their time hooting and therefore most activities were concentrated within or near activity centers. After this, hooting diminished as breeding activities declined, and males used areas outside activity centers more extensively. This change in behavior may explain the inverse relationship between size of area occupied and amount of time spent hooting: males that hoot the least may spend a greater proportion of time outside activity centers.

Territories of male blue grouse apparently function primarily as areas for display and breeding. Since territorial males spend most of their time during peak breeding within activity centers, what areas should be considered the territory: should the activity center alone be considered the territory or should areas occupied outside the activity center also be included?

Wilson (1975), Brown (1975), and Morse (1980), among others, define territory as an essentially exclusively occupied area which is either actively or passively defended. Other, less restrictive, definitions also have been proposed (see Kaufmann 1983 for a review). Overlap of adjacent areas of occupancy was uncommon and small even when all locations from radio-tagging until moving to new areas in summer were included. The small degree of overlap that occurred seems inconsequential given that sightings covering a span of over three months were included. As well, areas outside activity centers have been seen to be defended (Falls and McNicholl 1979, pers. obs.). Thus, I suggest that the total area occupied until moving to new areas following the breeding season was a "territory".

The activity center appears to be the focal point of the territory, however, as males concentrate their activity there during the period of peak breeding. As well, activity centers usually are situated on the most elevated portion of the territory, presumably facilitating the broadcasting of song and the detection of predators and conspecifics. The height of activity centers in relation to surrounding areas appears to be the most critical characteristic distinguishing between territorial sites of high and low quality (Lewis 1981, 1984b).

Nevertheless, if areas outside activity centers are defended this raises questions concerning the function of territories. Assuming that activity centers are sufficient as areas for display and mating, are areas outside them defended because they serve as buffer zones, or alternatively because they are needed as feeding areas? Presently, I do not have the necessary information to address this question.

I found no relationship between my measure of male aggressiveness and size of territory they occupied. Aggressiveness was related to size of area occupied during the breeding period, but only when the two males that were not hooting before playback experiments were conducted on them were excluded. This finding contrasts with that of Bergerud and Hemus (1975) in which territory size was related to aggressiveness. Their results may not be comparable to mine, however, as they compared mean size of territories of males from three different populations, each of which had different levels of aggressiveness; my comparisons were among individuals from a single population. Also, Bergerud and Hemus used the distance between the two most separate points of observation for each territorial male as an index of territory size, rather than measuring territory size *per se*, as I did. My results should be considered tentative, however, as sample size is small, only one experiment was conducted on each male, and only one measure of aggressiveness (response to playbacks) was used.

Why might territory size not be related to aggressiveness, as reported for red grouse (*Lagopus lagopus scoticus*) (Watson and Miller 1971)? Differences between species may be a consequence of different mating systems. Red grouse generally are monogamous (Wiley 1974) and females utilize resources found on territories. Males with the largest territories, however, sometimes acquire two mates

(Watson and Miller 1971), and therefore having large territories seems advantageous for species with such a mating system. In contrast, blue grouse are promiscuous and females do not remain on territories of males after breeding. Large territories for this species, then, may not confer any reproductive advantage; instead, features of the activity center, such as relative height, are likely more important.

Summary

Ten territorial male blue grouse (*Dendragapus obscurus*) were equipped with radio-transmitters on Hardwicke Island, British Columbia in April 1981 to monitor their movements throughout spring and summer. During peak breeding, males occupied areas that averaged 0.63 ha in size, and they usually remained near areas where they hooted (sang). After this time, areas of occupancy increased and season-long territory size averaged 1.9 ha. Territory size was not related to male aggressiveness, as measured here, but was inversely related to the amount of time residents spent hooting. Adjacent territories that overlapped did so by only 7.1% of their total areas, and there was no overlap of areas within which males hooted. Males remained on territories almost exclusively until abandoning them after the breeding season. Individuals varied in the time they abandoned territories, ranging from mid-June to mid-August. The entire area occupied until moving to new locations in early to late

summer was considered the territory, but the activity center, or area where hooting occurred, appeared to be the focal part of the territory.

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Table 1: Numbers of observations and sizes of areas (ha) occupied by radio-tagged males during the breeding (8 April to 20 May) and post-breeding (21 May to 16 June) periods, 1981. Observations of males away from territories excluded.

	Time period			
	8 April to 20 May		21 May to 16 June	
Male	No. obs.	Size of area occupied	No. obs.	Size of area occupied
667	19	0.44	21	0.29
668*	19	0.93	8	0.36
669	19	0.58	18	0.16
671	16	0.26	18	1.46
673	21	0.73	19	1.55
674	16	0.64	20	2.14
675	22	0.65	23	1.53
677	8	0.87	14	1.95
679	16	0.62	20	0.93
770*	16	0.60	11	0.34
Mean	17.2	0.63	17.3	1.07

*killed by predators; 668 on 31 May, 770 on 3 June.

Table 2: Numbers of observations, dates of territorial abandonment, and sizes of areas (ha) occupied until territorial abandonment for 8 radio-tagged males in 1981. Males killed by predators and observations of males away from territories excluded.

Male	No. obs.	Size of area occupied	Date of territorial abandonment
667	44	0.91	25 June*
669	72	1.68	11 August
671	49	2.13	16 July
673	48	2.11	4 July*
674	36	2.23	17-18 June*
675	63	2.00	20 July
677	25	2.75	25 June*
679	40	1.31	27 June
Mean	47.1	1.89	7 July

* date estimated.

Table 3: Aggression scores and proportion of observations in which radio-tagged males were hooting during the periods 8 April to 20 May, 21 May to 16 June, and 8 April to 16 June, 1981. Numbers of observations in parentheses; observations by workers that were not radio-tracking excluded.

		Proportion hooting		
Male	Aggression score*	8 April to 20 May	21 May to 16 June	8 April to 16 June
667	2	0.63(16)	0.14(21)	0.35(37)
668	7	0.31(16)	0.25(9)	0.28(25)
669	6	0.53(17)	0.17(18)	0.34(35)
671	0	0.39(13)	0.11(18)	0.23(31)
673	8	0.33(18)	0.05(19)	0.19(37)
674	5	0.21(14)	0.15(20)	0.18(34)
675	4	0.14(21)	0.22(23)	0.18(44)
677	0	0.00(8)	0.00(14)	0.00(22)
679	3	0.33(15)	0.10(20)	0.20(35)
770	1	0.67(12)	0.00(11)	0.35(23)
Mean	3.6	0.35(15.0)	0.12(17.3)	0.23(32.3)

*scores obtained by ranking responses to playback experiments; increasing scores indicate greater aggressiveness.

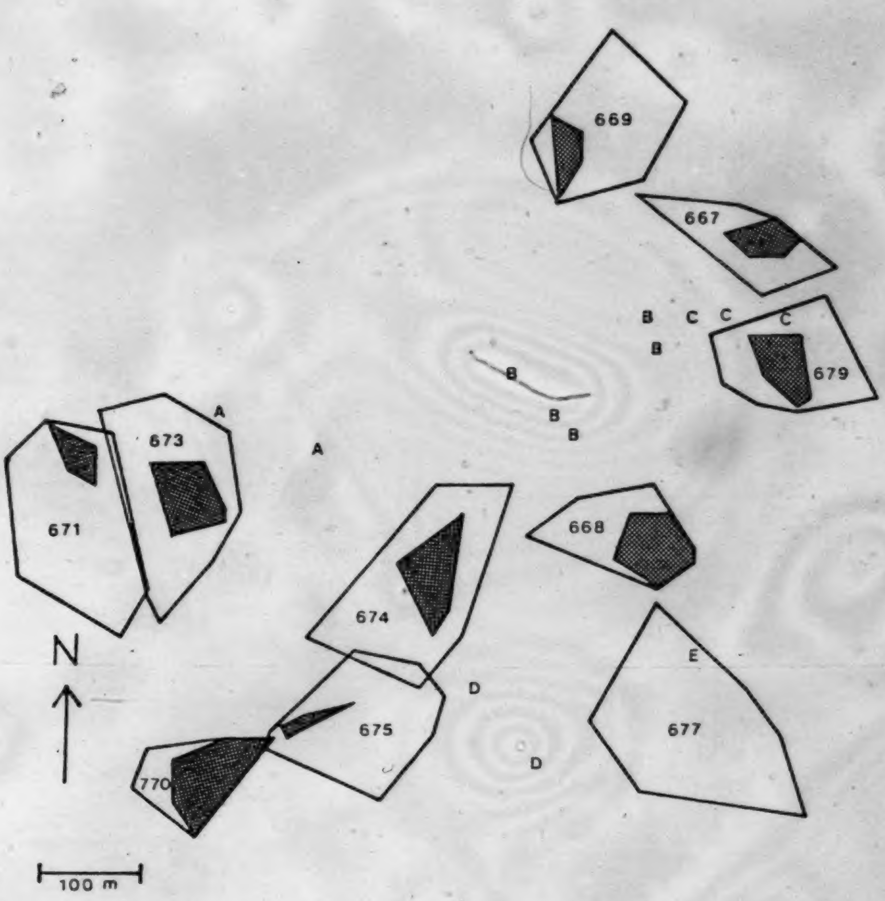

Figure 1. Spatial relationships of territorial males on Hardwicke Island, British Columbia in 1981. Total areas occupied by radio-tagged males until territories were abandoned are outlined with solid lines; areas within which males were observed hooting (singing) are shaded. Numbers identify individual radio-tagged males and letters indicate locations where non-radio-tagged territorial males were seen.

Paper 3: Behavior of male blue grouse and its relation to quality of territory occupied and attraction of females

Abstract

Relative aggressiveness and incidence of hooting were determined for territorial male blue grouse (*Dendragapus obscurus*) on a 95 ha area on Hardwicke Island, British Columbia, in 1980 and 1981. I then tested the hypotheses that the most aggressive males occupied the best areas for territories, and that males on high quality territorial sites hoot (sing) more than those on low quality sites. Aggressiveness of residents, as measured here, and quality of territorial site occupied were not correlated in either year. If my measure of relative aggressiveness of males reflects differences that were present among them prior to taking territories, then aggressiveness did not appear to affect a male's ability to obtain a prime site; movement patterns and experience as a yearling, when non-territorial, may be more critical. In 1981, but not 1980, males on high quality sites hooted more than those on low quality areas, and in that year more females were sighted near males that hooted the most. Males, therefore, may enhance their ability to attract females by hooting more than others, and this may be a characteristic of males occupying the best territorial sites. Thus, behaviors of males, as yearlings or adults, may affect individual reproductive success by influencing

success in acquiring high quality territorial sites and attracting females.

Introduction

Female choice of mates can be influenced by a male's behavior (Searcy 1979a, Weatherhead and Robertson 1979) as has been documented for red-winged blackbirds (*Agelaius phoeniceus*) (Weatherhead and Robertson 1977, Searcy 1979b, Yasukawa 1981). Differences among males in behavior, therefore, can result in individual variation in reproductive success. The mating system of blue grouse (*Dendragapus obscurus*) is considered to be promiscuous (Wiley 1974) and males occupy mating- and display-type territories from which they hoot (sing) to attract females and indicate their presence to other males (Bendell and Elliott 1967, McNicholl 1978). Thus, male behavior also may affect female choice of mates in this species. Further, sites used for territories differ in quality (Lewis and Zwickel 1980, 1981), suggesting that there may be competition for the best sites. Knowing this, two questions arise: 1) what determines which males acquire high quality sites?, and 2) can their behavior affect success in attracting females?

Males occupying high and low quality territorial sites did not differ in body weight (Lewis and Zwickel 1981), and no differences in weights of body organs were found between original and replacement birds that were removed from territories (Lewis and Zwickel 1980). However, in the latter study, replacement males had smaller testes than original occupants. Although cause and effect cannot be distinquished, this raises the possibility that aggressive tendencies may affect an individual's ability to acquire a specific territorial site. A number of workers have examined the effect of aggressiveness on territory acquisition with equivocal results (e.g., Watson and Miller 1971, Yasukawa 1979, Watson and Parr 1981, Searcy 1981). The relationship between aggressiveness and acquisition of territorial sites has not been investigated for blue grouse.

If females are preferentially attracted to certain males because of their behavior, what behavioral traits are most important? One function of song is to attract females (Catchpole 1982) and a male's quality may be assessed through his singing (Whitney and Krebs 1975, Kroodsma 1979, Yasukawa 1980, Fairchild 1981, West *et al*. 1981, Greig-Smith 1982). Thus, hooting behavior of individual male blue grouse may affect their ability to attract females.

The main objective of this study was to test the hypothesis that males occupying high quality sites are more aggressive and hoot more than those on low quality sites. As well, I examined locations of females in relation to those of males that differed in aggressiveness and percent of time spent hooting, and in relation to territorial sites of different quality. The objective was to determine whether females might assess the quality of a male on the basis of his behavior or on the basis of the quality of territorial site he had obtained.

Study area and methods

The study was conducted on Hardwicke Island (50°27'N, 125°50'W), which lies between Vancouver Island and mainland British Columbia, in the coastal western hemlock (*Tsuga heterophylla*) biogeoclimatic zone (Krajina 1965). The study plot was a recently (1968-1973) logged 95 ha area known as Lake Road. Dominant trees were Douglas fir (*Pseudotsuga menziesii*) and western hemlock. The most prevalent herbs and shrubs were ferns (*Polystichum munitum, Struthiopteris spicant, Pteridium aquilinum*), salal (*Gaultheria shallon*), fireweed (*Epilobium angustifolium*), and red huckleberry (*Vaccinium parvifolium*).

Field work was conducted from late March or early April to late July each year from 1980 through 1982. Searches were carried out almost daily with birds being found by listening for their hooting or by a trained pointing dog. As many birds as possible were captured with noose poles (Zwickel and Bendell 1967) and individually color-banded. Locations and identities of all birds sighted were recorded. Repeated sightings of individual territorial males were used to pinpoint the locations of their activity centers (Lewis and Zwickel 1981). If a known resident was not hooting I searched the immediate area with the dog.

The proportion of time individual males spent hooting was determined as I searched the study area. At hourly intervals, I recorded which males were and were not hooting of those that I could have heard from where I was at the time. The area was searched systematically so that all territories were covered relatively equally. Monitoring of the amount of time individuals spent hooting was begun on 3 May in 1980 and 16 April in 1981. It began earlier in 1981 because the identities and locations of most territorial males were known when field work began in that year.

Relative aggressiveness of males was assessed by conducting playback experiments on each of them; aggressiveness is defined here as the tendency to attack (Watson and Parr 1981). Two experiments were conducted on each male each year. Initial trials in 1980 were conducted between 1 and 10 May and replicates between 10 and 18 May; corresponding dates for 1981 were 16 to 25 April and 25 April to 5 May. Experiments were performed within the activity centers of the males' territories, and males had to be hooting prior to being tested. All experiments were conducted before 8:00 or after 18:00 hrs; males first tested in the morning had second tests in the evening, and *vice versa*.

In each experiment, the subject male was approached with as little disturbance as possible and a speaker and model of a male in display were placed approximately 10 m away and out of sight. I then moved another 10 m away and hid behind vegetation. After 10 min I played a tape of an unfamiliar male's hooting. For the next 10 min I recorded the type and timing of all responses by the resident. The same recording of hooting, but different models, were used in the two replicates in 1980, whereas different models and recordings were used in the two trials in 1981.

Of 28 territorial males present in 1980, 22(79%) were captured and banded by 26 April. From then until 18 May, I did not attempt to capture the remaining territorial males as playback experiments were conducted during that time. Three of the remaining unmarked individuals were captured and banded after 18 May. Twenty-one (84%) of 25 territorial males present in 1981 had been marked in 1980. I did not capture the four unmarked males in that year to avoid the possibility that catching and handling them would affect their incidence of hooting or response to playback experiments relative to males that did not have to be caught.

Results of a previous removal experiment conducted on Vancouver Island indicated that males preferentially selected areas for territories that were considered to be of high quality (Lewis and Zwickel 1980). To determine site quality at Lake Road, I conducted a similar experiment in 1982 in which original occupants and subsequent replacements were removed from territories. I assumed that territorial sites receiving replacement males were preferred, and hence higher in quality, than those with no relacements (Lewis and

Zwickel 1980).

I compared the number of female sightings that were nearer activity centers of occupied high quality territorial sites to the number nearer activity centers of occupied low quality sites to determine whether females were attracted to the highest quality areas prior to breeding. Only sightings obtained prior to the estimated date of breeding (Zwickel 1977) were used for females for which I knew the date on which their nest hatched. For females without known hatch dates I used only sightings obtained prior to the end of the two week peak breeding period (Zwickel 1977) in each year. Similarly, I examined locations of females to see if they were attracted to the most aggressive males or to males that hooted the most.

Results

Proportion of time hooting

Proportion of time spent hooting was determined for 25 males in 1980 and 21 in 1981; 14 individuals were monitored in both years. No data were collected for a few males either because they occupied relatively inaccessable areas (one each in 1980 and 1981) or because I was unsure of their identity until late in the spring (two in 1980). Three males died in early spring 1981 and no data were available for them.

Males varied greatly in the proportion of observations in which they were hooting (Figure 1). Most observations were made between 9:00 and 16:00 hrs (69 and 74% in 1980 and 1981, respectively) when hourly prevalence of hooting is relatively constant (McNicholl 1978). Mean number of observations per male was 49.6 ± 3.8 (S.E.) in 1980 and 81.8 ± 5.9 in 1981. Sample sizes varied among individuals because distances over which they could be heard varied depending on topography.

The mean proportion of observations for which males were heard hooting was lower in 1980 than 1981 ($t = -2.74$, $p = 0.009$, Figure 1). The difference probably is due to the earlier commencement date for monitoring hooting in the second year; peak hooting occurred from late April to early May in both years and hooting was monitored for only part of this period in 1980. There was no difference between years during the period 15 May to 25 June (0.23 ± 0.03 for 1980 and 0.26 ± 0.03 for 1981; $t = -0.632$, $p = 0.53$). Frequency of hooting of individual males present in both years was significantly correlated ($r = 0.581$, $0.02 < p < 0.05$).

Relative aggressiveness

Playback experiments were conducted on 23 males in 1980 and 20 in 1981; 12 individuals were tested in both years. Responses varied from nil to approach and repeated attack on the model. I scored each male on a scale of zero to six, depending on the level of response (Table 1).

Responses were reduced greatly in second tests in both years with the majority of males (N = 15 and 10 in 1980 and

1981, respectively) showing no response. Mean responses for the first and second tests were 3.6±0.5 and 1.0±0.4 in 1980, and 3.0±0.5 and 0.9±0.3 in 1981. Responses were normally distributed in initial trials but not in replicates (due to the number of 0 responses); for most males I therefore used the response score from first trials. However, three males in 1980 and two in 1981 responded more vigorously in replicates than in initial trials. Since increased responses by these males were inconsistent with habituation shown by most males, I used the higher scores as a measure of their aggressiveness.

Habituation shown by males in second experiments within years did not extend between years. Mean response by males tested in both years was 2.9 in 1980 and 2.8 in 1981 (U = 71.0, p = 0.93). Individual responses between years were not correlated (Spearman's rho = 0.39, p = 0.21), mainly because two males that did not respond, or responded weakly, in 1980, responded vigorously in 1981.

Behavior and Quality of Territorial Sites

Seventeen territorial males were present in 1982 and 14 were removed between 4 and 8 April. The remaining three were left on the area so that it would not be devoid of hooting males. Any males subsequently heard hooting on any of the 26 now vacant sites that had been used for territories between 1980 and 1982 also were removed.

A single replacement male was removed from each of eight territorial sites and two were removed from another. All replacement males, except one, settled on sites which had had territorial occupants originally present in 1982. I classified all sites receiving replacements as high quality. As well, prior to the removal in 1982, two males had changed the locations of their territories from one year to the next. Neither of the sites to which these males moved had replacements settle on them in 1982. However, I classified them as high quality because males that change territories usually move to high quality sites (Lewis and Zwickel 1981). This gave a total of 11 and 15 territorial sites that were considered high and low in quality, respectively.

In neither year was relative aggressiveness of a resident and quality of his territorial site related (Table 2). Quality of territorial sites occupied also was not related to proportion of observations in which residents were heard hooting in 1980, but in 1981 frequency of hooting was greater for males on high quality sites than for those on poor areas (Table 2). In neither year was there a correlation between an individual's relative aggressiveness and amount of time spent hooting (Spearman's rho = 0.158 and 0.142, p = 0.48 and 0.56 for 1980 and 1981, respectively).

Locations of Females

Ten and 15 high and low quality sites, respectively, were occupied in 1980; 51 sightings of females were nearer the former and 82 nearer the latter ($X^2 = 0.125$, $p = 0.72$). In 1981, 78 sightings of females were nearer the 11 occupied high quality sites and 46 nearer the 10 occupied low quality sites ($X^2 = 5.46$, $p = 0.02$). Thus, in 1981, but not 1980, females appeared to be attracted to areas where high quality territorial sites were located.

Males that were hooting in a greater proportion of their observations than the mean for the population within a year were classified as consistent hooters; those hooting less, sporadic hooters. Sixty-six sightings of females in 1980 were nearer activity centers of consistent hooters ($N = 14$) and 65 were nearer activity centers of sporadic hooters ($N = 11$), ($X^2 = 1.52$, $p = 0.22$). Corresponding figures for 1981 were 84 and 48 female sightings nearer activity centers of consistent ($N = 11$) and sporadic ($N = 10$) hooters, respectively ($X^2 = 6.83$, $p = 0.008$). Females, therefore, may have been attracted to males that hooted the most in 1981, but not in 1980.

I considered males that had response scores greater than three to be aggressive, and those having scores less than or equal to three, submissive. In 1980, 68 sightings of females were nearer activity centers of aggressive males ($N = 14$), 48 nearer activity centers of submissive males ($N = 9$) ($X^2 = 0.327$, $p = 0.57$). Nine males were considered aggressive and 11 submissive in 1981; respective numbers of female sightings nearer activity centers of these two groups of males were 59 and 68 ($X^2 = 0.127$, $p = 0.72$). Thus, in neither year did females show any significant attraction towards aggressive or submissive males.

Discussion

Before assessing results on aggressiveness, the effectiveness of playback experiments in measuring this behavior should be considered; that is, did they measure aggressiveness or a response to my presence? Some males that were difficult to approach when I searched the study area had high response scores in playback experiments, whereas others that were "tame", responded weakly or not at all. As well, I also conducted playback experiments in which female models and calls were used. Some individuals that responded weakly in male model experiments approached and displayed to female models; the converse also occurred. Therefore, I believe that differential responses to playback experiments represent differences in aggressiveness of the males, rather than reflecting differential responses to my presence. If true, there was no apparent relationship between a male's aggressiveness and the quality of territorial site he occupied. Caution should be used when interpreting these results, however, as sample sizes are small, only one measure of aggressiveness (response to playbacks) was used, and each male's relative aggressiveness was based on only one experiment.

An individual's aggressive tendencies may change, possibily due to experience and social interactions, and I measured aggressiveness of males after they had taken territories. However, if my measure of relative aggressiveness does, at least to some extent, represent inherent differences among males, then my results suggest that an individual's aggressiveness was not important in determining the quality of territorial site he obtained. If it is advantageous to obtain high quality territorial sites, why might the most aggressive males not be most successful in acquiring them? Jamieson and Zwickel (1983) found that individual yearling males, which usually are non-territorial (Bendell and Elliott 1967), had different patterns of movement in relation to territorial sites. They postulated that this could affect the quality of territorial site that is subsequently obtained. Similarly, Yasukawa (1979) found that experience with an area was more important than aggressiveness in determining whether or not male red-winged blackbirds acquired territories. Thus, whether male blue grouse acquire high quality territorial sites may be related to their behavior as yearlings. Getting there first also may be important. Once a territorial site is obtained, males usually are dominant there (e.g., Vos 1983) and residents may be able to expel intruders that inherently are more aggressive.

Males that occupied high quality sites in 1981 were seen hooting more often and had more females sighted near them than males on low quality sites. Were females attracted to individuals that hooted the most or were they attracted to areas where high quality sites were located? In a study on Vancouver Island, more females were found near territorial sites during breeding seasons in which they were occupied than in years in which they were vacant (Lewis 1979). This suggests that females are attracted by the presence of males. Hooting would seem to be a trait that females could use to assess male quality as, depending on topography, it can be heard over distances exceeding 500 m (Bendell and Elliott 1967, pers. obs.). Thus, assuming that characteristics of a male's hooting and his quality are related, females could assess the fitness of several males without having to be near them.

In conclusion, it appears that aggressiveness of males may not be important in acquiring high quality territorial sites or attracting females. Alternatively, behavior as a yearling, when non-territorial, may be most critical and future work on this aspect of blue grouse population ecology should concentrate on this age class. As well, males may enhance their chances of attracting females by hooting more than other males, and this may be a characteristic of males that occupy the best territorial sites.

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Table 1: Responses and assigned aggression scores for territorial males tested with playback experiments in 1980 and 1981 on Hardwicke Island.

Aggression score	Response
0	no approach; may alter hooting rate or orientation.
1	approach, but not to within 6 m of the model and speaker; no growling.
2	approach to 5 m or less but no growling.
3	approach and utter growls but remain near model or speaker for only a short time.
4	approach and circle or remain near model for prolonged period.
5	approach and weakly attack model by pecking or slapping it with wings.
6	approach and vigorously and repeatedly attack the model.

Table 2: Mean aggression scores and proportion of observations in which individuals were hooting for males occupying high and low quality territorial sites in 1980 and 1981. Sample sizes in parentheses.

		High quality sites	Low quality sites	P
Mean aggression score	1980	3.9±0.7(9)	4.1±0.6(13)	0.84
	1981	3.6±0.6(11)	3.0±0.7(7)	0.58
Mean prop. observations hooting	1980	0.30±0.04(10)	0.28±0.05(15)	0.71
	1981	0.44±0.04(11)	0.33±0.04(8)	0.05

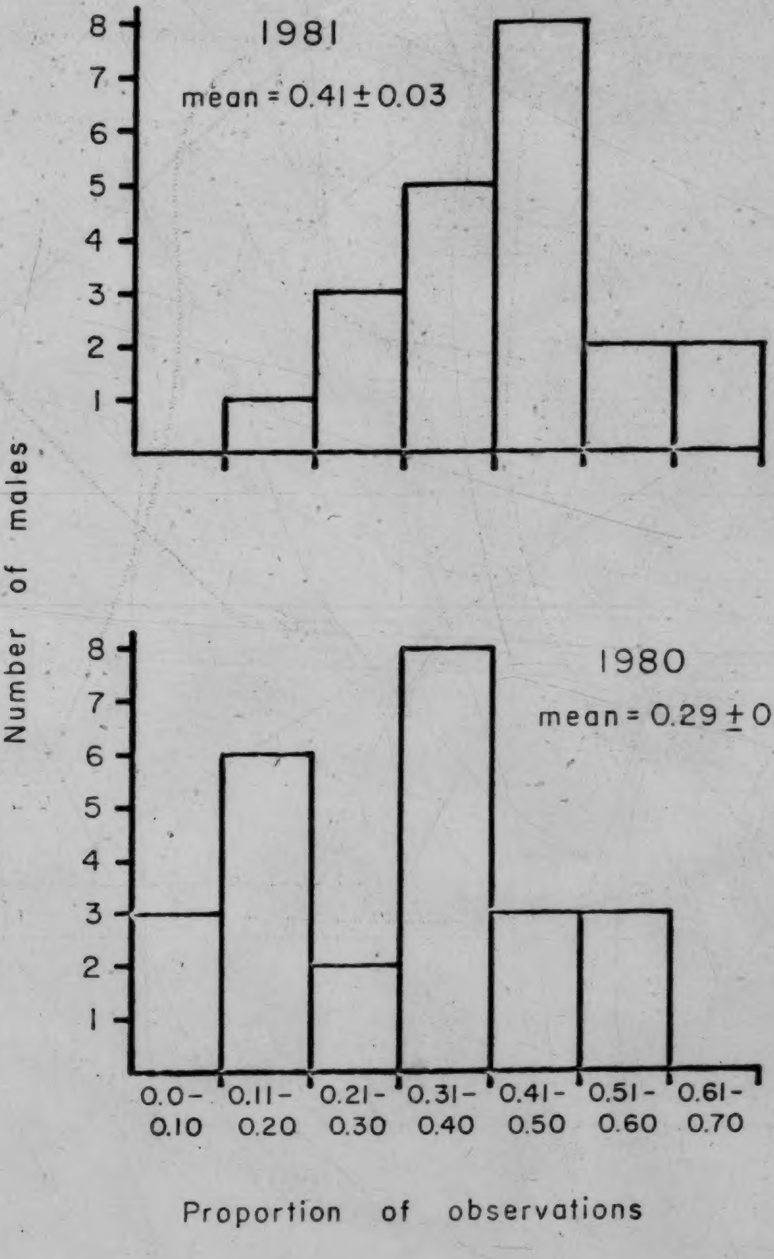

Figure 1. Proportion of observations in which individual territorial males were hooting in 1980 and 1981. Observations obtained up to 25 June only are included as hooting almost ceased after this time.

Paper 4: Density, movements, and breeding success of female blue grouse in an area of reduced male density

Abstract

The density of male blue grouse (*Dendragapus obscurus*) on a 95 ha area was reduced artificially by approximately 3/4 in 1982. Density and breeding success of females on this area in that year were compared to those of females on the same area in 1981 (when density of males was undisturbed) and to those of females on an unmanipulated control area in 1981 and 1982. As well, movements of females on the experimental area in 1982 were compared to those of females on that area in 1981 and to those of females on the control plot in 1982. A reduction in male density had no apparent effect on density of either yearling (recruits) or adult females, or on daily movements, timing of breeding, and breeding success of females. Home ranges of females were largest, but not significantly so, when male density was artificially reduced. The larger home range sizes of females residing in an area with a very low density of males did not seem to result entirely from females searching for males with which to breed. Results of this study suggest that densities of male blue grouse have no apparent effect on densities of females or production of young, and support the hypothesis that densities of females in this species are regulated independently of males.

Introduction

Past research that examined processes of animal population regulation often considered the role of only one sex, usually males. Many studies simply assumed that female densities were "tied" to those of males (Wynne-Edwards 1962). More recent studies, however, investigated the roles of both sexes (e.g., Fordham 1971, Boonstra 1978, Redfield *et al*. 1978a, 1978b, Clutton-Brock *et al*. 1982, Hannon 1983), and experimental reductions in densities of males have not affected those of females (e.g., Redfield *et al*. 1978a, b, Hannon 1983). These studies demonstrate that densities of females may be regulated by different means and independently of those of males (Redfield *et al*. 1978a, b).

Redfield *et al*. (1978a, b) and Hannon (1983) used single-sex-removal experiments to examine independence between densities of the two sexes. Here, I report on results of a similar experiment on blue grouse (*Dendragapus obscurus*) in which I removed males and examined effects on density and reproduction of females. Previous work suggested that densities of females may be regulated independently of males in this species (Hannon and Zwickel 1979, Hannon *et al*. 1982) and this experiment provided a more direct test of the hypothesis.

Background and Objectives

Male and female blue grouse migrate to breeding ranges in early spring and once there males establish territories from which they hoot (sing) to attract females and indicate their presence to other males (Bendell and Elliott 1967, McNicholl 1978). Most yearling (Bendell and Elliott 1967, Lewis and Zwickel 1981) and some adult (Lewis and Zwickel 1980) males do not take territories and are assumed to be non-breeders (Bendell and Elliott 1967, McNicholl 1978).

Adult females occupy restricted pre-nesting home ranges whereas yearling females move over larger areas until establishing residence in breeding populations (Hannon *et al*. 1982). No pair bonds are formed between males and females, and females generally occupy home ranges that are situated between or on the edge of male territories (Bendell and Elliott 1967, pers. obs.). This mating pattern is considered promiscuous (Wiley 1974) and females apparently choose among males for mates (Wittenberger 1978).

Intuitively, male densities might have greater effects on females of monogamous species than on those of polygynous or promiscuous species. However, numbers of males could affect females in the latter if yearling females (potential recruits) avoid areas where choices of breeding partners are restricted. Also, if male densities are reduced, older, resident females might move to areas of higher male density, or enlarge their home ranges so that they have access to more males. These situations could occur if breeding males differ sufficiently in quality to affect the quality of offspring produced by females (e.g., Weatherhead and Robertson 1979). Other potential effects of reduced male density on female reproduction include: 1) a delay in time of breeding if females spend more time searching for suitable breeding partners, and 2) lower hatchability or fertility of eggs resulting from any added stress of having to move more to find acceptable males with which to breed (Koenig 1982). The objective of this study was to determine if male density affected the density, pre-nesting movements, and/or breeding success of female blue grouse.

Study area and methods

This study was conducted on Hardwicke Island (77 sq km), which lies in Johnstone Strait between Vancouver Island and mainland British Columbia (50°27' N, 125°50' W), during the breeding seasons of 1981 and 1982. Two study plots, a control and experimental area, were used. Both were in various stages of regeneration following clearcutting between 1968 and 1973. The control area, situated on the west-central portion of the island, and the experimental area 0.65 km to the NE, were 470 and 95 ha in size, respectively. Vegetation structure on both ranged from "very open" to "dense" (Bendell and Elliott 1967), with western hemlock (*Tsuga heterophylla*) and Douglas Fir (*Pseudotsuga menziesii*) being the dominant overstory species. Primary understory species were fireweed (*Epilobium angustifolium*) and salal (*Gaultheria shallon*).

The experimental plot was an area I used for a study of behavior and use of territories by males (Lewis 1984), whereas the control plot was used for a more extensive study of population regulation in blue grouse (e.g., Jamieson 1983, Jamieson and Zwickel 1983). Census methods were similar on the two areas except that it was more intensive on the experimental plot, especially early in the spring. I searched the experimental area almost daily from early April to late August each year and two to three other observers searched the control plot beginning in early to mid-April and continuing through August. Trained pointing dogs were used to help find birds. Territorial males were found in spring, primarily by their hooting, and their numbers were counted directly.

Densities of females were estimated from sightings of individually color-banded birds. I believe that virtually all females were identified on the experimental area each year and direct counts were used as estimates of female numbers. Due to the less intensive search on the control area, estimates of female density there were based on the ratio of banded females seen both before and after broods hatched to those seen only after hatch (Redfield 1973).

Movements and home range sizes of females were determined using radio-telemetry. Radio transmitters were attached to nine adult females on the experimental area in 1981, and to 10 and 7 adult females on the experimental and control areas, respectively in 1982. Harness attachments (Herzog 1979) were used and radio-packages equalled 3-4% of a female's weight. Only adults were equipped with transmitters as this age-class was more likely to breed than yearlings (Hannon and Zwickel 1979).

Transmitters were applied to females between 9 and 21 April in 1981, and 6 April and 2 May in 1982. Radio-tagged females were located using a portable receiver and hand-held yagi antenna. Locations of females were estimated by measuring the distance and direction to known reference points. Females were found almost daily until initiating nests in 1981, and in 1982 they were found approximately 1-2 times daily on the experimental area and every 1-3 days on the control plot. Females were located more frequently on the experimental than control area in 1982 because I thought females there were more likely to make excursions to find males.

Home ranges of females were delineated using a minimum area method (Harvey and Barbour 1965), as modified by Sopuck (1979): outermost points of observation were connected only if distances between them were less than half the total range length. Sightings that were greater than half the range length from any other sighting were considered excursions (Harvey and Barbour 1965) and were not included in estimates of home range size. Mean daily movements were determined by measuring the distance between locations of individuals found on consecutive days (Herzog and Boag 1978). If a female was found more than once in a day her initial sighting was used as her location for that day.

Females were radio-tracked for different lengths of time depending on when they were radio-tagged and when they initiated laying. To standardize comparisons between areas and years, I restricted analyses to the 15 days prior to starting to lay. This period includes the time when females are in the rapid recrudescence phase of their ovarian cycle (9-10 days, Hannon *et al*. 1979) and when they breed (Zwickel 1977).

Data on dates of breeding, clutch sizes, and fertility and hatchability of eggs came from information on radio-tagged females, and females and nests found by observers working with dogs. If a hen's nest was not found, her hatch date was estimated by determining the age of her chicks (Redfield and Zwickel 1976) and backdating (Zwickel 1977). Only clutches known to be complete were used to determine mean clutch sizes. Fertility, as used here, is the percentage of eggs in a clutch that produced either chicks or unhatched embryos, and hatchability is the percentage of all eggs in a clutch that hatched (Zwickel 1975).

Results

Density of males

Densities of adult males on the control and experimental areas were similar within years (1981: 0.30/ha and 0.28/ha; 1982: 0.26/ha and 0.24/ha, respectively). Some adults on the experimental plot were considered non-territorial but data for males on the control area were insufficient to make such judgements on adults from there.

Of 17 territorial males (all adults) on the experimental area in early spring 1982, 14 were removed between 4 to 8 April, at least three weeks before breeding commenced. Another 10 males (six adults, four yearlings) took territories on sites from which males had been removed; all were shot, nine within a day of first being heard hooting. Four additional non-territorial yearling males were identified, but not removed. I believe that most non-territorial birds were identified and thus I reduced the total density of males (territorial and non-territorial combined) on the experimental area approximately 77% (24/31); the initial density of territorial (breeding) males was reduced 82% (14/17). Thirteen males that occupied territories in areas immediately surrounding the experimental plot also were potential breeding partners for females from that area. No males were removed from either area in 1981 or from the control plot in 1982.

Density of females and breeding success

Densities of combined adult and yearling females within years on the two areas were relatively similar (Table 1). Fewer females of both age classes were seen on the experimental area in 1982 than 1981, but similar declines occurred on the control area (adults: $X^2 = 0.187$, $p = 0.67$; yearlings: $X^2 = 0.238$, $p = 0.63$; Table 1). Percent yearlings was similar among areas and years ($X^2 = 0.478$, $p = 0.92$;

Table 1). Thus, a reduction in male density did not cause either resident or recruiting females to move elsewhere.

A higher proportion of adults (X^2 = 11.0, p = 0.001, both years combined) and a lower proportion of yearlings (X^2 = 4.72, p = 0.03, both years combined) were seen with broods on the experimental area compared to the control plot (Table 1). I believe that these differences result mainly from the lower intensity of search on the control plot, especially early in the spring, rather than reflecting real differences in breeding success.

Although estimates of percent females with broods differed between areas, there was no indication that a reduction in male density in 1982 affected breeding success of females on the experimental area. A similar percentage of adults and yearlings were seen with broods in the two years (adults: X^2 = 0.393, p = 0.53; yearlings: X^2 = 0.010, p = 0.922), as was the case for the control area (adults: X^2 = 0.643, p = 0.42; yearlings: X^2 = 1.70, p = 0.19) (Table 1). The higher proportion of adults with broods as compared to yearlings may have resulted from the failure of some yearlings to breed (Hannon and Zwickel 1979).

Daily movements

Radio-tagged females on the control area rarely were found on consecutive days, so comparisons of mean daily movements were made for females on the experimental area only. During the 15 days before starting to lay, females moved mean daily distances of 117 ± 13 m in 1981 ($\bar{x}$ = 9.1 consecutive day sightings/female) and 128 ± 24 m in 1982 ($\bar{x}$ = 10.5 consecutive day sightings/female; $t = -0.397$, $p = 0.70$) . Thus, females had similar mean daily movements on the experimental plot in the two years.

Home ranges

Home ranges on the experimental area during the 15 days before laying averaged 0.99 ± 0.23 ha ($\bar{x}$ = 11.2 sightings/female) and 1.75 ± 0.47 ha ($\bar{x}$ = 12.7 sightings/female) in 1981 and 1982, respectively ($t = -1.45$, $p = 0.17$). Females were radio-tagged later, on average, on the control than experimental area, and only five had sufficient numbers of sightings to examine size of home ranges. These females had mean home ranges of 0.76 ± 0.18 ha ($\bar{x}$ = 10.2 sightings/female), which was not significantly different from those of females on the experimental area in 1981 ($t = 0.676$, $p = 0.50$) or 1982 ($t = 1.96$, $p = 0.08$).

Six sightings involving five females and four involving four females were considered excursions on the experimental area in 1981 and 1982, respectively ($X^2 = 0.678$, $p = 0.41$); respective mean lengths of these movements were 165 ± 34 m and 377 ± 182 m ($U = 14.00$, $p > 0.20$).

Timing of breeding and nesting parameters

Median hatch date on the experimental area was 13-14 June (N = 34 females) in 1981 and 16 June (N = 29 females) in 1982. Similarly, hatching occurred earlier on the control area in 1981 than 1982 (median = 13 June (N = 123 females) and 15 June (N = 103 females), respectively).

Mean clutch sizes were similar among areas and years except for 1981 on the control plot (Student-Newman-Keuls multiple comparison test, $p < 0.05$, Table 2). Percent hatchability ($X^2 = 5.79$, $p = 0.12$) and fertility ($X^2 = 2.02$, $p = 0.57$) of eggs did not differ among areas and years (Table 2). Thus, reducing the density of males had no apparent effect on timing of breeding or nesting parameters.

Discussion

Neither density, recruitment, daily movements, nor timing of breeding were affected when approximately 3/4 of the males were removed from the experimental plot. As well, females were equally successful at nesting and producing young irrespective of whether or not the density of males was reduced artificially. Thus, density of male blue grouse does not appear to have an immediate influence on density of females or production of young. Further studies are required to determine whether there are long-term effects on recruitment of females or quality of offspring resulting from reduced choices of breeding partners.

Females on the experimental area in 1982 had home ranges that were approximately twice the size of those of females occupying areas with unmanipulated male densities (experimental area 1981 and control area 1982), and this difference approached significance. Given the small sample sizes of radio-tagged birds, there may be real differences between removal and non-removal situations. If so, there are three possible reasons for larger home range sizes on the experimental area: 1) females moved over larger areas looking for males so as to increase their choice of potential mates, 2) females used areas that would have been occupied by removed males, or 3) the number of females declined from 1981 to 1982 and individual females in the latter year may have been able to occupy larger areas.

Only two radio-tagged females on the experimental area in 1982 enlarged their home ranges into areas where territorial males were located; others, that occupied larger areas than females in 1981, had home ranges that did not overlap or lie adjacent to territories of males. Thus, larger home ranges in 1982 apparently did not result entirely from females searching for more males.

Not all territorial males were identified often enough in either year to determine the size of their territories. As well, except for two, different females were radio-tagged on the experimental area in 1981 and 1982. Therefore, I cannot evaluate the possibility that females used areas in 1982 that normally would have been occupied by males that were removed in that year. Also, although females appeared to use areas in 1982 that had been used by territorial males in 1981, the effect of this on the enlargement of female home ranges cannot be distinguished from the effect of a lower density of females in the second year. It is likely, however, that a complete explanation for the apparent difference in home range sizes between females residing in areas with reduced male densities and those on areas with normal male densities involves a combination of all three suggested causes.

Some females that produced young on the experimental area in 1982 occupied home ranges that neither overlapped nor were adjacent to territories of any males. With whom did these females breed? The three territorial males left on the area and 13 adjacent to it, were within a few hundred meters of the home ranges of most females, and home ranges of all females were within hearing distance of at least one hooting male. Females may have made quick movements to these males, copulated, and returned without being detected. Some females did make excursions, but if these represent moves to areas where hooting males were located such moves apparently also occurred in 1981 when male density was normal. Perhaps females can assess the fitness of territorial males through characteristics of their hooting (which can be heard over distances exceeding 500 m, depending on topography (Bendell and Elliott 1967, pers. obs.)), which would negate the necessity of occupying areas adjacent to territorial males.

In both years, I may have missed females making these movements if they usually were made during the early morning and/or late evening, as most radio-tracking was conducted during the day. A second possible means by which females on the experimental area in 1982 could have bred was by mating with non-removed, non-territorial males. This alternative seems less likely than the former one, however, as all known-aged non-territorial males were yearlings.

In summary, results of this study indicate that recruitment of yearling females and, in general, movements of resident adults were not affected when male densities were artificially reduced. Nor was there any apparent effect on production in the population. Thus, my results are similar to those of Redfield *et al*. (1978a, b) and Hannon (1983) and provide further support for the hypothesis that densities of females in blue grouse are independent of male density. They also suggest that sexually independent processes of population regulation can occur irrespective of whether a mating system is promiscuous (this study) or monogamous (Hannon 1983). Redfield *et al*. (1978a, b) and Hannon (1983) also reduced densities of females with no apparent effects on densities of males. Such an experiment on blue grouse would be useful in adding to our understanding of how densities of this species are regulated.

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Table 1. Numbers of females, percent yearlings, and percent seen with broods (in parentheses) on the experimental and control study areas on Hardwicke Island in 1980 and 1981.

	Experimental Area		Control Area	
	1981	1982	1981	1982
No. of adults	44(80%)	38(74%)	206(56%)	160(60%)
No. of yearlings	15(27%)	12(25%)	77(44%)	50(56%)
Total females	59	50	283	210
Density of females (number/ha)	0.62	0.53	0.60	0.45
% Yearlings	25	24	27	24

Table 2. Mean clutch sizes and percent fertility and hatchability of eggs on the experimental and control areas on Hardwicke Island. Sample sizes in parentheses; some unhatched eggs from the control area were not checked for fertility.

	Experimental Area		Control Area	
	1981	1982	1981	1982
Number of nests	8	9	24	29
Mean clutch size	5.4±0.3	5.4±0.3	5.8±0.2	5.6±0.2
% Hatchability	91.9(33)	94.3(35)	88.5(104)	81.2(133)
% Fertility	93.9(33)	97.1(35)	93.9(99)	90.7(107)

Paper 5: Habitat preferences of territorial male blue grouse

Abstract

Habitat characteristics were measured and compared for 28 sites used for territories by male blue grouse (*Dendragapus obscurus*) and for 10 areas not used for territories on a 95 ha area on Hardwicke Island, British Columbia, from 1980-1982. Among sites used for territories, comparisons also were made between those that were preferred and non-preferred. Habitat variables measured were: "relative height", slope, ground level visibility, amount of cover, and dispersion of cover and open areas. Territorial and non-territorial sites differed only in their relative heights and degrees of slope; territorial sites were greater in both respects. Preferred territorial sites had greater relative heights and ground level visibility, and less cover, than non-preferred sites. Cover also tended to be most clumped on preferred sites. When distinguishing between areas that were and were not suitable for territories, males appeared to discriminate primarily on the basis of topographic characteristics. Topography also appeared to affect the quality of sites that were suitable for territories, but at this level of selection vegetative features also may have been important.

Introduction

Several workers have examined habitat selection by blue grouse (*Dendragapus obscurus*) in coastal British Columbia (Bendell and Elliott 1966, 1967, Redfield *et al*. 1970, Zwickel and Bendell 1972, Donaldson and Bergerud 1974, Niederleitner 1982). The approach in those studies was to describe habitat characteristics of areas with different densities of blue grouse. Additionally, I compared topographic and vegetative features of territorial sites of males that differed in frequency of use and apparent quality (Lewis 1981). To date, however, habitat characteristics of territorial sites of coastal blue grouse have not been compared quantitatively to areas not used for territories, as was done for blue grouse in Montana (Martinka 1972).

Territories of blue grouse serve primarily as areas where males attract and display to females, although feeding and other activities also occur there (Bendell and Elliott 1967, McNicholl 1978). Blue grouse have elaborate courtship displays (Hjorth 1970, McNicholl 1978) and these may be facilitated by the presence of open areas. Conversely, cover may enhance escape from predators, and its amount will be inversely related to degree of openness. If both cover and open areas are important components of territorial sites, their dispersion may affect site quality more than does either of their absolute amounts. In my previous study (Lewis 1981), I found no difference in amount of cover or open areas on high and low quality territorial sites (persistent and transient sites, respectively), but at that time I did not measure their dispersion.

The objectives of the present study were to quantitatively compare habitat features of territorial sites and areas not used for territories, and to compare the dispersion of cover and open areas on high and low quality territorial sites. As well, this study was done on a different area, Hardwicke Island, than my previous one, Comox Burn, Vancouver Island, and I compare and discuss results from the two areas.

Study area and methods

Hardwicke Island lies in Johnstone Strait between Vancouver Island and mainland British Columbia (50° 27' N, 125° 50' W), in the coastal western hemlock (*Tsuga heterophylla*) biogeoclimatic zone (Krajina 1965). I studied aspects of male territoriality from 1980-1982 on a recently logged 95 ha area situated on the north-central portion of the island. This area, known as Lake Road, had a vegetative structure ranging from "very open" to "dense" during this time (see Bendell and Elliott 1967 for a description of terms) and general exposure was N-facing. Dominant trees were western hemlock and Douglas fir (*Pseudotsuga menziesii*); hemlock regeneration was natural but most firs were planted. Primary herbaceous and shrubby species were fireweed (*Epilobium angustifolium*), ferns (sword fern, *Polystichum munitum*; deerfern, *Struthiopteris spicant*; and bracken fern, *Pteridium aquilinum*), salal (*Gaultheria shallon*), and red huckleberry (*Vaccinium parvifolium*).

Vegetation and topography at Lake Road and Comox Burn were relatively similar except that terrain on Lake Road was more broken and western hemlock was more prevalent. Also, Comox Burn had been burned by a wildfire whereas Lake Road had undergone controlled slash burning.

I searched Lake Road almost daily from late March to late July each year. Territorial males were found by listening for their hooting (singing) or by a trained pointing dog. Areas where hooting (territorial) males were found were searched repeatedly throughout spring and summer to determine the locations of individual territories.

Theoretically, food will be a necessary component of the habitat of any species (Hilden 1965). However, food does not seem to be limited in habitats used by blue grouse in coastal British Columbia (Zwickel and Bendell 1972), and neither quality nor quantity of food appears to affect densities of territorial males (Ash 1979). I therefore only measured habitat variables that might affect a resident's ability to avoid predators or to attract and display to females. All measurements were made within activity centers, the area within territories where most hooting occurs (Lewis and Zwickel 1981).

Most territorial sites of blue grouse are located on heights of land, such as hills, knolls, and ridges (Bendell and Elliott 1966, 1967; Figure 1). Topographic features measured were slopes around, and "relative heights" (Lewis 1981) of, activity centers; these could affect the propagation of hooting as well as the ability to detect predators and conspecifics. Slopes were estimated by measuring the incline of a string stretched between two poles held upright and 10 m apart. Four measurements were made in each activity center and their sum was used as an index to the slope of that site. The first measurement was in the direction of the general exposure of the site, the three others at 90°, 180°, and 270° to this; uphill slopes were assigned negative values. Relative height, which is the horizontal distance from the activity center of a site to the nearest area of equal height (Figure 1), was estimated by stereoscopic analysis of aerial photographs. This gives a measure of the height of the activity center in relation to surrounding areas and serves as an index to the distance that the resident's hooting may be heard.

Ground level visibility, which could affect the likelihood of detecting females, intruding males, or predators (Donaldson and Bergerud 1974, Lewis 1981), was measured with a cover board (De Vos and Mosby 1971). The board was 30.5 x 30.5 cm with a pattern of eight red and eight white squares. It was placed on the ground at 5 m intervals from the spot where the resident most frequently hooted, out to 40 m, in each of the four cardinal compass directions. An observer, simulating the position of a grouse on a stump at the hooting site, counted the number of squares that were at least 50% visible at each location. This number gave a relative measure of ground level visibility within a site.

Amount of cover and its dispersion were measured using a combination of a modified canopy cover method (Daubenmire 1959) and Pielou's (1977:144) method for measuring dispersion of dense and sparse grid cells. A 20 m square matrix consisting of 100, 2 m x 2 m blocks was established on each territory, centered at the location where residents were most frequently seen hooting on each territorial site. Percent cover within each 4 m^2 block was classified using Daubenmire's rating scale: 1=0-5%, 2=6-25%, 3=26-50%, 4=51-75%, 5=76-95%, 6=96-100%. Anything that would provide concealment for a grouse on the ground was considered cover, e.g., vegetation, logs, etc. The midpoint percent of each cover class was used as the percent cover for each block, and percent cover within an activity center was estimated as the mean of the 100 blocks.

Dispersion of cover was quantified by classifying each block as being either cover (>50% cover) or open (≤50% cover) and counting the number of "cover blocks" that adjoined each other (Pielou 1977). An expected value and a variance for the number that would have adjoined if they were distributed randomly was calculated for each site. Dispersion was quantified as observed minus expected number of adjoining cover blocks divided by the variance. A value of 0 represents a random distribution and values above and below this a tendency towards clumping and uniform spacing, respectively. Since cover and open areas may not be distributed similarly, I repeated the procedure to quantify dispersion of open areas.

Studies at Comox Burn indicated that frequency of occupancy was related directly to the quality of territorial sites (Lewis and Zwickel 1980, 1981). To determine site quality at Lake Road I removed original occupants and subsequent replacements from most territorial sites in 1982. A few sites were left occupied so that the area would not be devoid of hooting males. Sites receiving, and not receiving, replacements were classified as high and low quality, respectively (Lewis and Zwickel 1980).

In addition to measuring habitat variables on territorial sites I randomly selected 10 areas that were not used for territories during 1980-1982 and measured habitat variables on them. Variables involving vegetation were measured in April and May 1982, before herbaceous growth began developing rapidly. Comparisons were made between territorial and non-territorial sites, and within territorial sites, between those of high and low quality. These comparisons represent two phases of selection by males: first, selection for areas that are suitable for territories, and second, selection among acceptable sites for those that might best enhance opportunities for breeding and surviving.

Student's *t*-tests were used to compare means of individual variables and significance was accepted at the 0.05 probability level. Habitats of territorial and non-territorial sites and of high and low quality territorial sites also were compared using a stepwise discriminant function analysis (Nie *et al.* 1975). Caution should be used when interpreting results of this analysis, however, as sample sizes were small (Magnusson 1983). Therefore, in the discussion I will consider only results of individual comparisons.

Results

Numbers of territorial males declined from 28 to 17 between 1980 and 1982, and 29 different territorial sites were occupied in the three years. I removed 14 of the 17 original territorial males in early April 1982, thus leaving 26 territorial sites vacant. Subsequently, one replacement was removed from each of eight sites, and two were removed from another. All replacements, except one, settled on sites from which original occupants had been removed in 1982. I classified all sites receiving replacements as high quality. In addition, in both 1981 and 1982 one male moved to a different territorial site from the one occupied the previous year. Neither moved to a site that received a replacement in 1982 but I classified these sites as high quality because other data indicate that when males change territories they usually move to high quality areas (Lewis and Zwickel 1981). Thus, 11 and 15 sites were considered of high and low quality, respectively. I refer to these as "preferred" and "non-preferred" sites. Habitat variables were measured on all sites classified for quality, and on two of the three sites from which original occupants were not removed in 1982.

Territorial vs. non-territorial sites

Both topographic variables, slope and relative height, were significantly greater on territorial than non-territorial sites (Table 1).

Over 75% of the "visible" squares on the cover board were from locations within 15 m of the observation point. I therefore compared visibility on territorial and non-territorial sites within both 15 and 40 m of the observation point. Neither were significantly different although differences in visibility within 40 m approached significance (Table 1); the tendency was for visibility to be greater on non-territorial sites. Neither amount of cover nor dispersion of cover or open areas differed between territorial and non-territorial sites (Table 1).

Territorial and non-territorial sites were classified with 89.5% accuracy when they were compared with the stepwise discriminant function analysis. In descending order, slopes, dispersion of open areas, visibility within 40 m, and relative height contributed significantly to discriminating between the two types of areas.

Preferred vs. non-preferred territorial sites

Relative heights of preferred sites were greater than those of non-preferred sites, but slopes did not differ (Table 2). Thus, among areas used for territories, males preferred those that did not have areas of equal or greater height nearby.

Visibility within 15 m of the observation point was significantly greater on preferred than non-preferred sites, and approached significance within 40 m (Table 2). Percent cover also was significantly different and differences in dispersion of cover were nearly significant: preferred sites had less cover and it tended to be more clumped than on non-preferred sites (Table 2). Dispersion of open areas did not differ between the two types of site (Table 2).

Stepwise discriminant function analysis was 84.6% accurate in classifying territorial sites as being of high or low quality based on the seven variables measured. Variables contributing significantly to the discrimination in descending order were: relative height, slope, dispersion of open areas, and dispersion of cover.

Discussion

At the initial level of territorial site selection, that is, when distinguishing between areas that were and were not suitable for territories at Lake Road, males apparently based their selection primarily on topographic characteristics; vegetative features appeared to be of lesser or no significance. However, among areas that were suitable for territories, differences in quality were related to both topographic and vegetative features of the site. Social influences of conspecifics also may affect habitat selection and preferences (Hilden 1965), but none were examined in this study.

Ultimately, selection likely is based on the integration of a number of variables. For example, both cover and open areas may affect territorial site quality. However, since amount of cover and open areas are inversely related, both their amount and dispersion may be important, as appeared to be the case at Lake Road. Also, some habitat variables, such as amount of openness, may affect survival and breeding success in opposite ways. Areas that provide the combinations of features that best enhance survival and breeding success should be preferred.

The only significant difference I found between high and low quality sites on Comox Burn was that it was farther from the former to areas of equal or greater height than for the latter (Lewis 1981). At Lake Road it also was farther from preferred territorial sites to areas of equivalent elevation than for non-preferred sites, suggesting that this may be a generalization for blue grouse in logged habitats in coastal British Columbia.

In contrast to Comox Burn, preferred and non-preferred territorial sites at Lake Road also differed with respect to visibility and amount of cover. Cover also tended to be more clumped on preferred than non-preferred sites at Lake Road but its dispersion was not measured on Comox Burn.

Ground cover was greater on territorial sites at Lake Road than on Comox Burn (Table 1, present study; Table 1, Lewis 1981), at least partly due to the fact that the wildfire on Comox Burn consumed most of the slash and created large areas of bare ground that were slow to revegetate. As well, natural revegetation of trees was greater at Lake Road than on Comox Burn. Perhaps greater ground cover at Lake Road resulted in it becoming more important in territorial site selection and preferences than on Comox Burn; as vegetation becomes too dense males stop recruiting to areas used previously (Bendell and Elliott 1967, Redfield *et al*. 1970).

In conclusion, coastal male blue grouse appear to select areas for territories mainly on the basis of topography. Topography also appears to affect the quality of sites that are selected for territories. Vegetative features may affect territory site quality in some habitats, and differences among habitats in this respect may be related to the amount of ground cover.

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Table 1. Topographic and vegetative characteristics (Mean ± S.E.) of territorial (N = 28) and non-territorial (N = 10) sites on Lake Road, Hardwicke Island. See text for description of measurements.

Habitat characteristic	Territorial site	Non-terr. site	P
Relative height (m)	118.5±28.1	14.0±7.2	0.001
Slope (degrees)	45.6±4.3	2.6±4.5	0.000
Visibility within 40 m	51.7±6.1	75.0±13.6	0.082
Visibility within 15 m	41.6±4.2	56.7±11.3	0.235
Percent cover	50.4±3.4	48.1±5.2	0.723
Dispersion of cover	1.12±0.24	1.25±0.26	0.765
Dispersion of open areas	1.46±0.22	1.19±0.29	0.516

Table 2. Topographic and vegetative characteristics (Mean ± S.E.) of preferred (N = 11) and non-preferred (N = 15) territorial sites on Lake Road, Hardwicke Island. See text for description of measurements.

Habitat characteristic	Preferred site	Non-preferred site	P
Relative height (m)	206.8±61.4	53.1±12.0	0.034
Slope (degrees)	50.3±8.0	41.9±5.0	0.362
Visibility within 40 m	65.0±9.5	41.5±7.8	0.066
Visibility within 15 m	52.1±5.4	32.1±4.8	0.011
Percent cover	42.6±4.4	56.1±4.3	0.044
Dispersion of cover	1.32±0.23	0.70±0.21	0.062
Dispersion of open areas	1.30±0.41	1.49±0.28	0.696

COLOURED PICTURES
Images en couleur

A

B

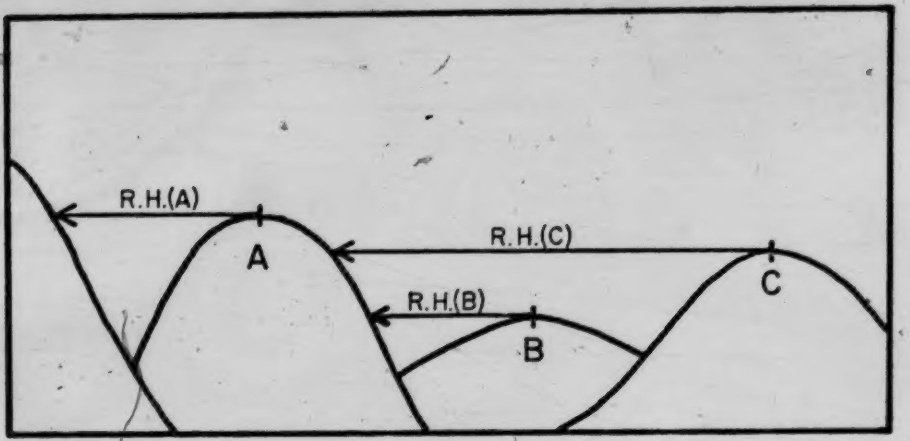

Figure 1. A. General habitat of the study area; numbers indicate locations of territorial sites. B. Graphic illustration of the measurement of relative height (R.H.) of territorial sites (A, B, C), relative height being the horizontal distance from the activity center of the site to the nearest area of equal height.

Concluding Discussion

General

A central problem in ecology is to explain how densities of animals are determined. Many factors, such as food, weather, predators, etc., have been postulated to impose limits on densities of breeders (Andrewartha and Birch 1954, Lack 1954, 1966, Clark *et al*. 1967). Some workers, however, have suggested that densities of breeders are controlled intrinsically through physiological, behavioral, or genetic means (Pimental 1961, Christian and Davis 1964, Chitty 1967, Brown 1969, Krebs 1978, 1979). These 2 views have been distinguished as the extrinsic and intrinsic schools of thought. In the latter, intrinsic mechanisms are believed to maintain densities of breeders below levels at which extrinsic factors become limiting.

When intrinsic mechanisms are invoked as the means by which densities of animals are determined, the proposed mechanism often is said to operate in relation to some external resource (e.g., Watson and Moss 1968, 1972, Taitt 1981, Taitt and Krebs 1981, Taitt *et al*. 1981). Also, it likely is not advantageous for individuals to defend more resources than are required for survival and reproduction (Tullock 1978, MacLean and Seastedt 1979, Pleasants and Pleasants 1979). Hence, densities of most, if not all populations likely are limited, ultimately, by external factors. Population ecologists thus appear to be asking 2 questions: 1) what factor(s) limit densities of breeders in a specific area or at a specific time (=limitation), and 2) what mechanism(s) maintain breeding populations within these limits (=regulation). I will refer to these as limiting factors and regulating mechanisms, respectively. Often no distinction is made between them and this can lead to confusion (e.g., Watson and Moss 1970). Collectively, they explain how densities of breeders within an area are determined.

Population studies of blue grouse

Blue grouse (*Dendragapus obscurus*) have been studied in coastal British Columbia since the early 1940's, with the overall objective being to explain how densities of breeders are determined (e.g., Fowle 1944, Bendell and Elliott 1967, Zwickel and Bendell 1972, Zwickel *et al*. 1983). The importance of extrinsic factors and intrinsic mechanisms both have been examined (e.g., Bendell 1955, Zwickel and Bendell 1967, Mossop 1971, Bendell *et al*. 1972, Redfield 1972, Zwickel 1972, Bergerud and Hemus 1975, King and Bendell 1983), with more recent studies emphasizing the role of behavioral mechanisms (Hannon and Zwickel 1979, Lewis and Zwickel 1980, Zwickel 1982, Hannon *et al*. 1983, Jamieson and Zwickel 1983). Results of these studies suggest that densities of breeding males and females may be regulated independently (Hannon and Zwickel 1979, Lewis and Zwickel 1980, Hannon *et al*. 1983). In this investigation, I studied aspects of territorial behavior in males and looked for effects of male densities on those of females. Here, I integrate my results with those of others and discuss how densities of breeding male blue grouse might be determined.

Background

Blue grouse are considered to have a promiscuous mating system (Wiley 1974a, Wittenberger 1978) in which males occupy mating- and display-type territories (Bendell and Elliott 1967); occupancy of a territory is considered necessary for breeding (Bendell and Elliott 1967, McNicholl 1978). Sites used for territories apparently differ in quality, with males that occupy the best sites seemingly having the best opportunities for breeding (Lewis and Zwickel 1980, 1981).

Although vacant, low quality sites usually, or always, are available (Lewis and Zwickel 1981), most yearling (Bendell and Elliott 1967) and some adult (Lewis and Zwickel 1980, 1982, Jamieson and Zwickel 1983, Appendix I) males do not take territories. Non-territorial males have smaller testes than adults, but are physiologically able to breed (Hannon *et al.* 1979, Lewis and Zwickel 1980); non-territorial males thus delay breeding. Densities of breeding males will be affected by the number of individuals that do not take territories, so the reason why some males defer breeding is integral to understanding how numbers of breeders are determined.

Evolution of delayed breeding in male blue grouse

Two hypotheses have been proposed to explain why delayed breeding has evolved in some male grouse (Wiley 1974a, Wittenberger 1978). Wiley postulated that risks associated with holding a territory and attempting to breed may be greater for young, inexperienced males than for older individuals. He also suggested that breeding success might be related to age and experience, with older males most successful. He demonstrated that delayed breeding could evolve if early survival and/or later reproduction were enhanced by not breeding at the earliest possible age (Wiley 1974b).

Wittenberger hypothesized that delayed breeding evolved solely as a consequence of sexual selection. He argued that in species in which female choice of mates occurs, there is competition among males for access to females. Young males, having less experience, likely would be less successful than older males in attracting for females and delayed breeding would evolve.

Both hypotheses predict that any loss of fitness incurred by postponing breeding would be more than compensated for by benefits of enhanced future breeding success; lifetime breeding success thus would be maximized (Selander 1965). A third hypothesis explaining the basis for delayed breeding, but which is untestable, has been proposed by Mason (1979). He suggests that prolonged immaturity is a mechanism that promotes phenotypic flexibility which in turn is "the mainstay of the evolutionary process".

Yearling males do not exhibit the full range of courtship behaviors shown by adults when they interact with females (Jamieson 1982), thus they likely would not be successful in competition with adults for females. This supports Wittenberger's hypothesis. However, if males delay breeding primarily as a consequence of sexual selection, most, if not all, yearlings should take territories when adults are removed. Some yearlings did take territories when I removed adults but many others did not. As well, some yearlings have home ranges that encompass only vacant territorial sites (Jamieson and Zwickel 1983). If Wittenberger's hypothesis was correct, yearling males that exhibit this spatial pattern should have taken territories on vacant sites, since they likely would settle in the same areas as adults (Sopuck 1979, Jamieson and Zwickel 1983). Thus, it seems unlikely that delayed breeding evolved in male blue grouse solely as a consequence of sexual selection.

In attempting to refute Wiley's hypothesis, Wittenberger assumed that there were no risks associated with territorial and breeding activities. He cited experiments in which yearling male blue grouse took territories when adults were removed (Bendell and Elliott 1967, Zwickel 1972, Bendell *et al*. 1972) as providing direct support for his hypothesis.

When he assumed that there were no risks associated with territorial and breeding activities, Wittenberger did not consider that areas used for territories might differ in quality. Current evidence indicates that sites used for territories do differ in quality (Lewis and Zwickel 1980, 1981), and survival of residents apparently is related directly to the quality of site that is occupied (Lewis and Zwickel 1981, 1982). Differences in survival of residents on high and low quality territorial sites might result from differences in the topography and vegetative structure of these areas (Lewis 1981, 1984a). Non-territorial males thus risk higher mortality if they take territories on vacant, poor quality areas. In addition, because males tend to remain on the same territory for life, the increased risk of mortality associated with taking territories on poor areas early in life would persist into the future. Early breeders also could suffer higher mortality than older males due to lack of experience, irrespective of the quality of territorial site that is acquired, but information needed to test this possibility is not now available for blue grouse. There is evidence, however, that non-territorial males survive as well as territorial males (Lewis and Zwickel 1982, Appendix I), and hence there are no apparent costs associated with not having a territory; this contrasts with reports for red grouse (*Lagopus lagopus scoticus*) in which non-territorial birds suffer high rates of mortality (Watson 1964).

Males on high quality territorial sites also may have more opportunities for breeding than those on poorer areas as females are seen near them more frequently (Lewis and Zwickel 1981, Lewis 1984b). Differences in amount of time spent hooting (singing) by males possibly affects their success in attracting females, and males on high quality sites may hoot the most (Lewis 1984b). Differences in behavior among males therefore, may affect success in attracting females, and this could in part be related to age and experience. Whether attracting more females results in greater breeding success has not been determined, so it is not possible to draw definite conclusions regarding differential breeding success of males on high and low quality territorial sites at this time.

I suggest that male blue grouse delay breeding because early survival and possibly later reproduction are enhanced by doing so, as suggested by Wiley (1974a). Increased risks and lower potential for breeding associated with breeding at an early age appear to be related to inexperience and quality of territorial sites that would be obtained. The relative importance of these factors may differ depending on age; e.g., yearlings may delay breeding primarily because of increased risks arising from inexperience whereas young adults may not take territories mainly because they are unable to obtain high quality sites. In both of my removal experiments, most replacement males were adults, and no adult was known to remain non-territorial when high quality sites were available.

What determines densities of breeding male blue grouse?

Many workers have examined the role of territorial behavior, and other forms of spacing behavior, in regulating densities of breeding animals (e.g., Hinde 1956, Brown 1969, Watson and Moss 1970, Klomp 1972). Territorial behavior may play a role in regulating densities of breeding male blue grouse, but other behaviors also appear to be involved.

Most high quality territorial sites are occupied each year and territorial behavior by resident males prevents additional males from settling on these areas. Excluded males must either settle on low quality sites or remain non-territorial. Their choice may depend on their behavior as yearlings. For instance, Jamieson and Zwickel (1983) found that yearling males exhibit different patterns of movement and they postulated that some associate with a limited number of high quality territorial sites (Type A pattern) and that others localize around low quality sites (Type B pattern). Type A yearlings would be more likely to obtain high quality territorial sites than those of Type B. However, since males on high quality sites survive better than those on poorer areas, the probability of territories becoming vacant within the home range of Type A yearlings is relatively low. Thus, both costs and benefits of Type A patterns are higher than those of Type B (Jamieson and Zwickel 1983). The number of young adults that delay breeding therefore, may relate to the number of yearlings that adopt Type A patterns, and that subsequently are unable to obtain a territorial site in the area they occupied as a yearling. Behavior of both yearlings and adults thus appears to be part of the mechanism that regulates densities of breeding males. Individual aggressiveness may not be important in this process as playback experiments indicated that quality of territorial sites was not correlated with relative aggressiveness of residents (Lewis 1984b). Aggressiveness of residents and territory size also does not appear to be related (Lewis 1984c), which again differs from findings on red grouse (Watson and Miller 1971). Bergerud and Hemus (1975) found a direct relationship between territory size and aggressiveness of residents in another population of blue grouse. However, their "estimates" of territory size were home range lengths, not areas, and their numbers of locations per male were much smaller than the numbers of observations I had available.

What ultimately limits densities of breeding males? Brown (1969) suggested that non-breeders or "surplus" birds should not be present in populations unless all optimal and marginal habitats are filled. If non-breeders are present suitable habitat may be limiting. High and low quality territorial sites seem equivalent to optimal and marginal breeding habitat for male blue grouse, yet some males do not take territories (are non-breeders) even though suitable, but low quality, areas always are available. Thus, availability of suitable sites for territories would not seem to be limiting densities of breeding males. However, high and low quality territorial sites differ vegetationally and topographically in ways that might affect survival and breeding success of residents (Lewis 1981, 1984a). If breeding is limited to males on high quality sites, densities of breeding males may be limited by numbers of high quality sites present. If this is not the case, however, their availability likely is not the ultimate factor that limits densities of breeding males.

Numbers of territorial males at Lake Road on Hardwicke Island dropped from 28 in 1980 to 17 in 1982. Even with a 39% decrease in numbers of territorial males, some adults still delayed breeding (Appendix I). Perhaps numbers of adults that delay breeding are related to numbers of females (i.e., potential mates). Alternatively, they may be related to the potential for breeding, which would be related to both numbers of male competitors and females. When male density was reduced artificially, no effect on female densities was observed (Lewis 1984d). However, the converse experiment, which would test for effects of female densities on males, has not been undertaken on blue grouse, as it has been on the monogamous willow ptarmigan (*Lagopus lagopus*) (Hannon 1983). If mechanisms that regulate densities of territorial males operate in response to densities of females, the factor(s) within the habitat that limits female densities also may, ultimately, limit densities of breeding males.

In summary, a combination of territorial behavior by adults and movements and behavior of yearlings appears to be the proximate intrinsic mechanism that regulates densities of breeding male blue grouse. This regulation is achieved in part through the process of delayed breeding. The extrinsic factor(s) to which this mechanism responds, and that ultimately limits densities of breeding males, is less well understood. Densities of females, and the factor(s) limiting their densities, may be important, however.

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Appendix I: Further evidence of non-territorial adult male blue grouse

Until recently it was believed that all adult male blue grouse (*Dendragapus obscurus*) held territories (Zwickel, J. Wildl. Manage. 36:1141-1152, 1972). However, it now has been reported that non-territorial adult males (≥ two years of age) are present in populations in coastal British Columbia (Lewis and Zwickel, Can. J. Zool. 58:1417-1423, 1980; Jamieson and Zwickel, Auk 100:653-657, 1983). Non-territorial males are presumed to be non-breeders (Bendell and Elliott, Can. Wildl. Serv. Rep. Ser. 4, 1967; McNicholl, Ph.D. thesis, Univ. Alberta, Edmonton, Alberta, 1978), and their presence raises questions that relate to the problem of explaining how densities of breeding males are regulated. Here, I present further evidence for the existence of non-territorial adult male blue grouse and provide information on their abundance within breeding areas.

I conducted an intensive study on aspects of territoriality in male blue grouse from 1980 through 1982 on a 95 ha area on Hardwicke Island (50°27'N, 125°50'W), British Columbia. I searched almost daily throughout the spring and summer to locate territorial males, these being individuals that were localized on small areas and that were heard hooting (singing) (Bendell and Elliott, 1967;

McNicholl, 1978). I believe I found all such males each year, of which over 80% were individually color-banded. These males were found repeatedly to establish the locations and extents of their territories.

Numbers of territorial males declined from 28 to 17 between 1980 and 1982, and all that were banded were adults. In addition, four marked adults in 1980 and two in 1981, were considered non-territorial. Three of these were seen only once but classified as non-territorial because they were captured on territories of other males during non-migratory periods. The other three were seen between three and eight times, and their movements were far ranging and similar to those of non-territorial yearlings (Sopuck, M.Sc. thesis, Univ. Alberta, Edmonton, Alberta, 1979; Jamieson and Zwickel, 1983). Another male, banded as a yearling in 1980 and not seen again until 1982, probably was non-territorial in 1981 because, in that year, all territorial males on and adjacent to the site on which he settled in 1982 were identified; on the rare occasions when males do change territories from one year to the next they usually move to adjacent sites (Lewis and Zwickel, Condor 83:171-176, 1981).

In 1982, I removed original occupants and subsequent replacements from 14 territorial sites. Six of 10 replacements were adults that were banded as yearlings in 1981. Five of these had been seen one to four times in other locations prior to settling on removal sites. In the absence of my removal experiment I believe that most of these birds would have remained non-territorial throughout 1982 since they took territories only after original occupants were removed. Thus, non-territorial adults were present each year even though the number of territorial males was declining.

Four of the six adults identified as non-territorial in 1980 and 1981 occupied territories in the subsequent year; all on sites on which they had been seen the year before. This is similar to reports that new territorial adults usually settle on sites within the area of their yearling home ranges (Sopuck, 1979; Jamieson and Zwickel, 1983). Although sample size is small, the mortality (disappearance) rate of non-territorial adults on Hardwicke Island was relatively low (2/6), as on Vancouver Island (Lewis and Zwickel, Can. J. Zool. 60:1881-1884, 1982).

Non-territorial males are not as easily identified as those on territories. This makes it difficult to determine precisely the percentage of young adults that are non-territorial. However, seven of eight males that first took territories during 1981 and 1982 had been banded earlier, and four were three years of age or older. Additionally, four of 10 males that were radio-tagged as part of another study on Hardwicke Island were non-territorial at two years of age (Jamieson and Zwickel, 1983). Thus, a substantial proportion of young adults appear not to participate in breeding. Why some adult males do not take territories, although vacant territorial sites always exist (Lewis and Zwickel, 1981), is a crucial question if we are to understand how densities of breeding males in this species are regulated.

Appendix II: Territorial sites of pallid blue grouse, *Dendragapus obscurus pallidus*

There are eight subspecies of blue grouse (*Dendragapus obscurus*) (Johnsgard 1983), which often are separated into two general groups: coastal (the *fuliginosus* group) and interior (the *obscurus* group), each consisting of four subspecies. These groups differ in several behavioral and morphological respects (Table 1).

I studied aspects of territoriality in a coastal subspecies of blue grouse, *D. o. fuliginosus*, from 1977 to 1983, mainly in areas that were in various stages of regeneration following clearcutting (Lewis 1981, Lewis and Zwickel 1980, 1981, this thesis). Sites used for territories appeared to be selected primarily on the basis of topographic features (Lewis 1984), and were distributed uniformly (Lewis and Zwickel 1981).

For three weeks in May 1983, I studied an interior subspecies, *D. o. pallidus*, in north-central Washington State and here report on findings relating to territorial site selection by males in this area. Most interpretations and comparisons with *D. o. fuliginosus* are qualitative as most data from Washington State were not collected in sufficient detail to permit quantitative evaluations.

I searched for territorial males in three general habitat types in Washington State: 1) coniferous forest consisting primarily of Ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*), 2) open shrub-grassland consisting primarily of *Artemisia tridentata, Purshia tridentata*, and native bunch grasses (*Agropyron spicatum, Poa secunda*, and *Festuca idahoensis*) with widely scattered thickets of aspen (*Populus tremuloides*) or conifers, and 3) forest-shrub-grassland edge which commonly had large open areas interspersed among patches of conifers. I found territorial males mainly by listening for their hooting (singing), and searching was concentrated in the mornings and evenings when incidence of hooting was greatest.

Territories in coniferous forest and forest-shrub-grassland edge generally were located in areas where openings were present. Similarly, territories of *D. o. fuliginosus* tend to be associated with open areas (Bendell and Elliott 1966, 1967, Lewis 1981, 1984). In open shrub-grassland most, but not all, territories had trees nearby (Figure 1). Territories here often were grouped around thickets of aspen or conifers, suggesting that these areas may be preferred by territorial males. However, not all aspen or conifer thickets had territorial males associated with them (Figure 1).

Twenty-five of 37 territories in Washington State were located on hills, knolls, or ridges. Territories of *D. o. fuliginosus* also tend to be associated with elevated areas (Bendell and Elliott 1966, 1967, Lewis 1981, 1984). The apparent preference for elevated areas, however, did not appear to be as pronounced in *D. o. pallidus* as in *D. o. fuliginosus*. Territories in Washington State that were not on elevated areas typically were located near thickets of trees. Thus, trees may be an important component of territories in these habitats (Martinka 1972), even though all territories did not have trees near them (Figure 1).

Thus, territorial site selection by *D. o. pallidus* generally appears similar to that of *D. o. fuliginosus*; that is, territories tend to be on open, elevated areas. However, vegetative characteristics may be more important in territorial site selection in interior habitats than in coastal areas. As well, territories in coastal areas were distributed uniformly (Bendell and Elliott 1967, Lewis and Zwickel 1981) whereas in open shrub-grassland in Washington State they tended to be clumped (R = 0.867, Clark and Evans 1954), although not significantly so (c = 1.57, $p > 0.05$) (Figure 1). This tendency toward clumping appears to result from males preferentially selecting territories near or adjacent to thickets of trees (Figure 1).

Quality of territorial sites in coastal British Columbia was related primarily to topographic characteristics, with vegetative features being of secondary importance (Lewis 1981, 1984). If vegetative features are more important in territorial site selection in interior habitats than in coastal habitats, this raises questions relating to which features affect territorial site quality most in the interior. Answering these questions likely would add greatly to our understanding of territorial site selection in blue grouse.

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Table 1. Behavioral and morphological differences between coastal and interior subspecies of blue grouse.

characteristic	coastal	interior
loudness of hooting (song)	loud	"soft"
frequency of flutter flights	frequent	infrequent
color of cervical apteria	yellowish	reddish
number of rectrices	usually 18	usually 20*
presence of tail band	present	absent or indistinct*

* with the exception of *D. o. obscurus* which has a wide, distinct tail band and usually 18 rectrices.

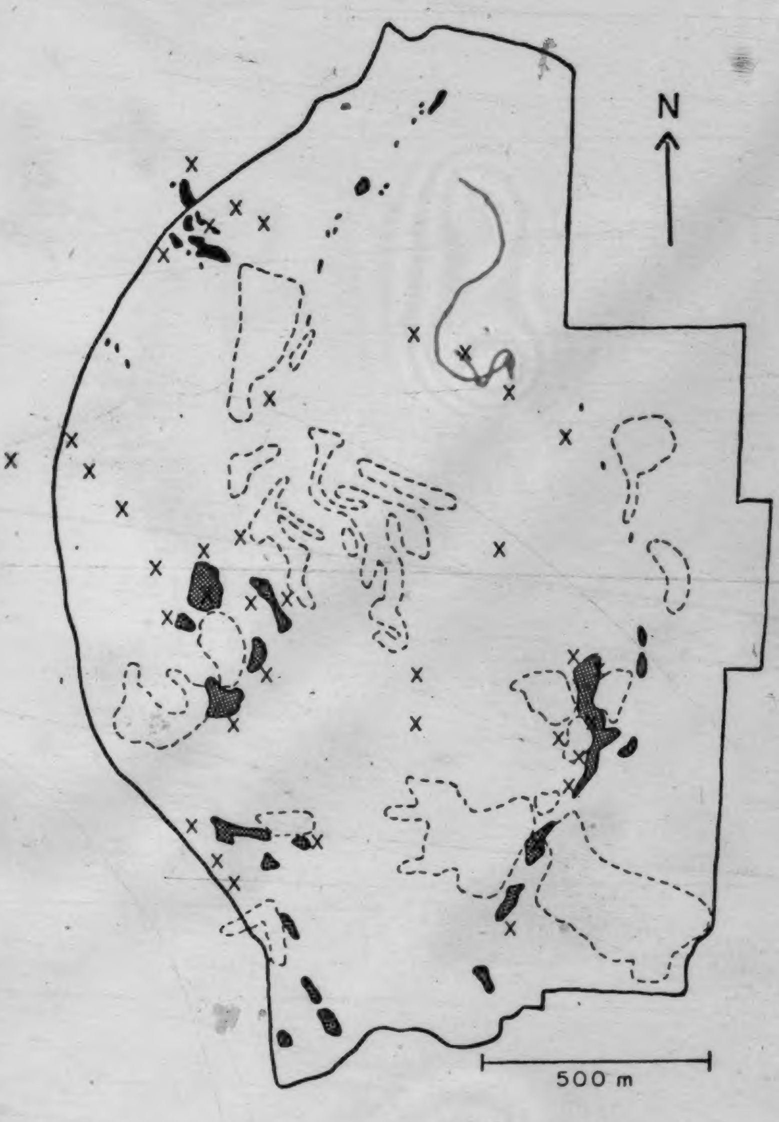

Figure 1. Vegetation types and location (X) of areas where individual males usually were hooting on Frazer Creek, Washington State, 1983. Darkly and lightly shaded areas are conifers and aspen, respectively. Agricultural fields are outlined with dashed lines. Unmarked areas are open-shrub-grassland, primarily composed of *Artemisia tridentata*, *Purshia tridentata*, and native bunch grasses.